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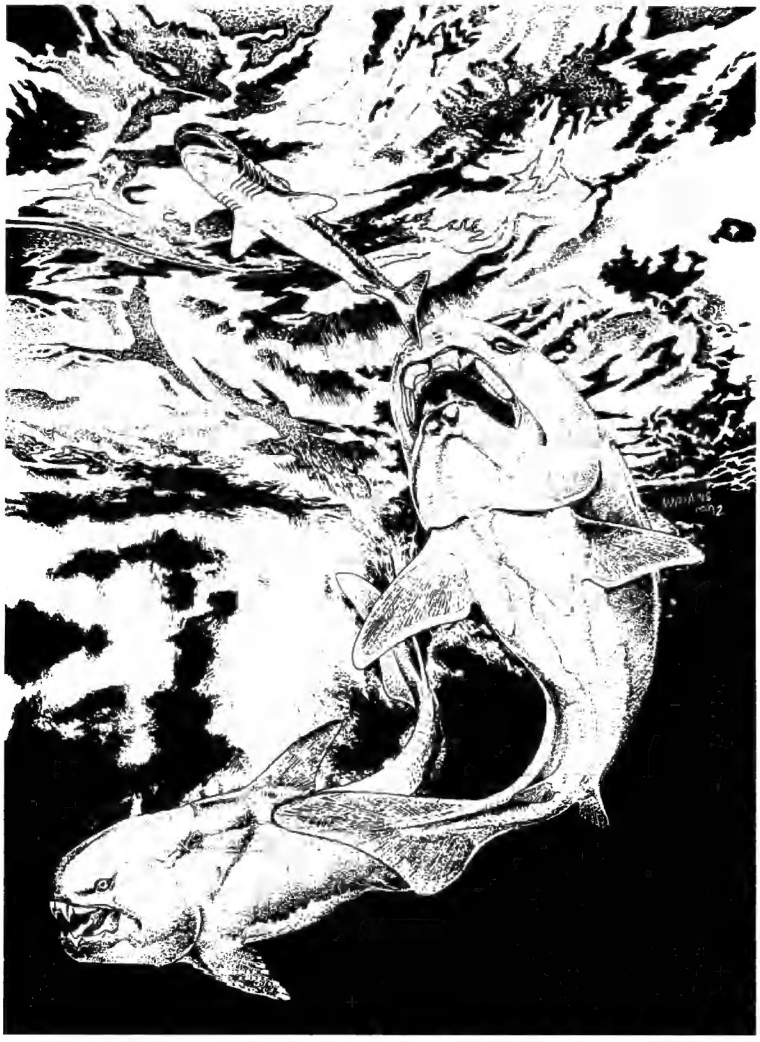
VIIe Symposium international, Parc de Miguasha, Québec

Études sur les Vertébrés inférieurs

Coordonné par Marius ARSENAULT, *Hervé* LELIÈVRE *et Philippe* JANVIER



Reconstitution de deux *Dunkleosteus terelli*, Placodermes géants poursuivant un *Cladoselache*.

Dessin de © Joseph WINANS

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VIIth International Symposium Studies on Early Vertebrates

9-22 June 1991, Miguasha Parc, Quebec

Marius ARSENAULT, Hervé LELIÈVRE and Philippe JANVIER
(Editors)

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VIIe Symposium international Études sur les Vertébrés inférieurs

9-22 juin 1991, Parc de Miguasha, Québec

Coordonné par Marius ARSENAULT, Hervé LELIÈVRE et Philippe JANVIER

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Études sur les Vertébrés inférieurs
Studies on Early Vertebrates

Coordonné par Marius ARSENAULT, Hervé LELIÈVRE et Philippe JANVIER
(Publié avec le concours du Ministère de l'Environnement et de la Faune, Gouvernement du Québec)

AVANT-PROPOS

Depuis le symposium international de Miguasha sur les Vertébrés inférieurs quatre années se sont écoulées. Ce n'est en effet qu'après un rude combat contre l'adversité économique que les contributions des participants à cette réunion peuvent enfin être publiées, grâce au *Bulletin du Muséum national d'Histoire naturelle*, Paris, et au soutien du Ministère de l'Environnement du Gouvernement du Québec : qu'ils soient ici remerciés.

On pourrait penser qu'un tel délai de parution rendrait désuets les articles présentés. Cela serait peut-être vrai dans d'autres disciplines, mais dans ce cas précis il n'en est rien. La plupart des contributions réunies dans ce volume sont des articles de fond, des descriptions anatomiques de base qui n'ont pratiquement pas pris une ride en quatre ans. Cette pérennité est, du reste, l'une des qualités des volumes issus de cette série de rencontres sur les Vertébrés inférieurs qui commença à Stockholm en 1967, puis se poursuivit par les symposiums de Londres (1973), Tallinn (1976), Canberra (1983), Pékin (1987), Tallinn (1989), Miguasha (1991) et cette année à Paris (1995). Ils restent toujours à portée de main des chercheurs qui travaillent soit sur les Vertébrés paléozoïques, soit sur les Vertébrés dits « inférieurs » actuels (globalement les poissons et les amphibiens). Les pages qui suivent contiennent par exemple la première description du squelette de l'un des plus anciens tétrapodes connus, *Acanthostega*, la description détaillée de l'anatomie de l'ostéolépiforme le mieux conservé connu à ce jour, *Medoevia*, ou encore la première description des Vertébrés ordoviciens et siluriens de Sibérie. D'autres articles proposent soit des analyses phylogénétiques de groupes, soit des analyses de la biodiversité d'environnements paléozoïques, soit encore des données d'ordre biologique sur les Vertébrés primitifs actuels.

Le site de Miguasha, qui a accueilli ce symposium, est l'un des plus riches gisements de Vertébrés dévoniens ; c'est à René BUREAU qu'il doit son statut actuel de parc protégé. Ce gisement a en outre livré les spécimens du poisson ostéolépiforme *Eusthenopteron foordi*, dont l'étude par le Professeur E. JARVIK, du Musée Suédois d'Histoire naturelle de Stockholm, a été la clé de la compréhension du passage de la vie aquatique à la vie terrestre chez les Vertébrés. C'est pour cette raison que le Professeur E. JARVIK, effectuant ainsi sa première visite sur ce site après un demi-siècle de recherches sur *Eusthenopteron*, était Président d'Honneur de ce symposium ouvert par le Professeur PAGEAU, autre pionnier auquel nous souhaitons rendre hommage.

Mais n'oublions pas tous ceux, nombreux, qui contribuèrent au succès de cette rencontre, par des « affiches » ou des communications publiées séparément (leur impatience ne peut certes être blâmée !).

Pour la postérité, ajoutons que lors de ces journées de juin 1991, sur le rivage de la baie des Chaleurs, le soleil était radieux et les homards succulents. L'accueil des habitants de Miguasha, dans la langue de Molière comme dans celle de Shakespeare, restera longtemps dans la mémoires des participants.

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Ordovician Vertebrates and Agnathan phylogeny

(A contribution to IGCP 328-Palaeozoic Microvertebrates)

by Pierre-Yves GAGNIER

Abstract. — The most complete Ordovician vertebrate known to date is *Sacabambaspis janvieri*. This jawless fish, like heterostracans, possesses dorsal and ventral shields made up of large median plates. Anteriorly, the dorsal shield delimits an elliptical space that contains the eyeballs with their dermal sclerotic and scleral ossifications, and the paired olfactory capsules. The anterior part of the ventral shield is composed of square-shaped platelets aligned in rows to form an exoskeletal mouth apparatus resembling that of heterostracans. *S. janvieri* may have a lateral series of 20 branchial plates and its bone is cellular. All the Ordovician vertebrates were previously classified with the heterostracans. Our present knowledge of the anatomy of the Ordovician vertebrates indicates that the Australian and Bolivian forms are more closely related to each other, forming a monophyletic group (Arandaspidiformes), than to the North American genera which are more closely related to the heterostracans. The Ordovician vertebrates may thus be united with the heterostracans into a monophyletic group, the Pteraspidomorphi. This does not invalidate the myopterygian concept, but reduces the importance of the involved characteristics. The analysis suggests that the presence of two olfactory capsules is primitive for vertebrates, as is also a single median narial opening.

Keywords. — Vertebrata, Agnatha, Ordovician, anatomy, relationships.

Les Vertébrés ordoviciens et la phylogénie des Agnathes

Résumé. — La morphologie la mieux documentée de Vertébrés ordoviciens est celle de *Sacabambaspis janvieri*. Elle montre la présence de deux boucliers médians couvrant le dessus et le dessous de la tête, d'une vingtaine de plaquettes marginales disposées en rangées obliques, de globes oculaires antérieurs, de deux dépressions juxtaposées en position pinéale et parapinéale, de hautes et fines écailles disposées en 4 rangs sur le pourtour du corps, d'une nageoire caudale diphycerque et d'un système de la ligne latérale bien développé. Ces données montrent que les formes australiennes et boliviennes ont entre elles des relations de parenté plus étroites qu'avec les genres nord-américains, *Astraspis* et *Eriptychius*. Une nouvelle définition des Heterostraci est avancée : elle exclut les taxa ordoviciens qui tous possèdent plusieurs orifices branchiaux externes. Le taxon Pteraspidomorphi est proposé pour l'ensemble des Vertébrés ordoviciens et des Heterostraci. Les Pteraspidomorphi sont caractérisés par une cuirasse externe composée d'au moins deux plaques osseuses médianes, à croissance concentrique. Enfin, les résultats de l'analyse phylogénétique produite n'invalident pas le concept de Myoptérygien, mais en réduisent de beaucoup son importance. La présence de deux capsules nasales semble être un caractère primitif pour l'ensemble des Vertébrés, au même titre que la présence d'un orifice nasal impair et médian.

Mots-clés. — Vertebrata, Agnatha, Ordovicien, anatomie, phylogénie.

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INTRODUCTION

Recent analyses suggest a closer relationship between the petromyzontids and gnathostomes than between the petromyzontids and myxinoids (LØVTRUP, 1977; JANVIER & BLIECK, 1979; JANVIER, 1981; FOREY, 1984). Historically, COPE (1889), GOODRICH (1930), STENSIÖ (1927), JARVIK (1964), or more recently YALDEN (1985) regarded agnathans as monophyletic. COPE

(1889) united the Heterostraci and Osteostraci, together with the Antiarchi (Placoderms) under the name Agnatha. Most recent and current phylogenetic reflections on vertebrates consider that the gnathostomes descend from a group of agnathan (LØVTRUP, 1977; JANVIER, 1978, 1981; JANVIER & BLIECK, 1979; HARDISTY, 1979; FOREY, 1984). The taxon Agnatha thus represents a paraphyletic group, contrary to the opinion of JARVIK (1967, 1968) or STENSIÖ (1964). Nevertheless, I shall use here this name for practical reasons, since it is well known, though referring to a grade.

The Heterostraci (pteraspids) and Osteostraci (cephalaspids) were formerly grouped with the Antiarchi in the "ostracoderms" because of their dermal bony armour, as opposed to the Cyclostomata, lampreys and hagfishes, which are boneless. Later the Antiarchi were recognized as gnathostomes and removed from the Agnatha. Because of their dermal armour, ostracoderms have been mainly classified on the basis of their type of armour growth.

Since STENSIÖ (1927) tried to demonstrate a relationship between cephalaspids and lampreys, the term "ostracoderm" refers to a paraphyletic group, and is no longer retained as a taxon. Nevertheless, it emphasizes on the problem of comparisons between boneless extant agnathans and armoured fossil agnathans. All phylogenetic schemes reflect this problem. The idea of a cephalaspid-lamprey sister-group relationship was long maintained and developed (JANVIER & BLIECK, 1979; JANVIER, 1980, 1981; HALSTEAD, 1982; BLIECK, 1982).

The inclusion of fossil taxa by STENSIÖ (1927) has reorganized agnathan phylogenetic topologies, with the Cephalaspidomorphi, which include the petromyzontids (lampreys), Osteostraci and Anaspida, as opposed to the Pteraspidomorphi, which include the myxinoids (hagfishes) and Heterostraci (STENSIÖ, 1927, 1964, 1968; JARVIK, 1964, 1968; ROMER, 1968; JANVIER, 1975b). The Cephalaspidomorphi are characterized by a nasal sac and a nostril opening that are median in position and confluent with the hypophyseal duct. They also possess muscularized fins and extrinsic eye musculature. The Pteraspidomorphi retain what is considered as a more primitive condition in which the nasal sacs and the external narinal openings are paired, as in the gnathostomes.

HALSTEAD (1973a, 1982) and NOVITSKAYA (1975, 1983) made restorations of the heterostracan olfactory organ, based on the gnathostome model. The suggestion of a paired olfactory organ did not receive great acclaim. Then, myxinoids and heterostracans where treated independently and Pteraspidomorphi became a synonym of Heterostraci. The term Pteraspidomorphi has thus been discarded. In contrast, JANVIER & BLIECK (1979) adopt a phylogeny where petromyzontids and gnathostomes are sister-groups. JANVIER (1981, 1984) included the Cephalaspidomorphi in the myopterygians and suggested a possible sister-group relationship between osteostracans and gnathostomes. One of their main ideas was a progressive development of muscular fins, from unpaired to paired.

The three-taxon phylogeny of extant craniates, including hagfishes, lampreys and gnathostomes, is not yet resolved. The addition of fossil agnathans does not increase the resolution. Moreover, as pointed out by SCHAEFFER & THOMSON (1980), the outgroup is uncertain. Cephalochordates, with their notochord, epichordal nervous system, metameric musculature, and branchial region, are convenient outgroups but are far from providing a suitable list of homologous characters. In this paper I do not intend to reconsider these problems. I shall instead focus on the implication of Ordovician vertebrates to our understanding of primitive vertebrate (agnathan)

relationships. A character analysis using PAUP software 2. 4. 1. for IBM compatible (SWOFFORD, 1985) was performed using a matrix (table 1) that includes different taxonomic levels. Cephalochordates were used as outgroup.

The fossil record of jawless fishes began when they evolved the ability to produce a bony armour. The following extinct taxa are recognized as Paleozoic agnathans: Heterostraci, Galeaspida, Osteostraci, Anaspida, Thelodonti. In addition the two extant agnathan taxa, myxinoids and petromyzontids, are known as early as the Carboniferous. Agnathans with dermal skeleton are known from the Ordovician to the Upper Devonian. Their greatest diversity was reached between the mid-Silurian and the late Devonian (Fig. 1), and they become extinct at the end of the Frasnian, in the late Devonian.

Three different epochs may be defined in agnathan history:

1. The Ordovician period, with the earliest known forms (Fig. 1), which is the main subject discussed here;

2. The Silurian-Devonian is the Golden Age of agnathans, which reached their highest diversity during this period. At the beginning of the Devonian, during the diversification of the gnathostomes, heterostracans almost disappear and are followed by the other groups of bony agnathans. One of these groups is the anaspids, but some authors consider anaspids as being more closely related to the Recent petromyzontids (STENSIÖ, 1927; WÅNGSJÖ, 1952; JANVIER, 1981; JANVIER & BLIECK, 1979; FOREY, 1984). This relationship is likely, but still supported by tenuous evidence.

3. Finally, the Carboniferous period provides the first record of the Myxinoidea, or Hyperotreti, and the Petromyzontida, or Hyperoartia (BARDACK, 1986, 1991; BARDACK & RICHARDSON, 1977; BARDACK & ZANGERL, 1971; JANVIER & LUND, 1983; LUND & JANVIER, 1986). These two groups are the only agnathans known from post-Devonian times.

Extant agnathans, lampreys and hagfishes, neither possess a dermal skeleton, nor paired fins. Their first appearance in the fossil record is also problematical. The resemblance of the

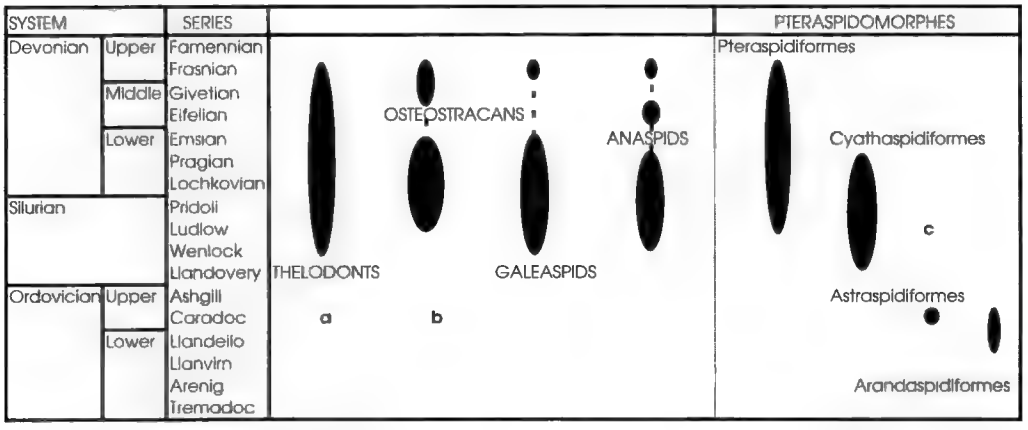

FIG. 1. — Stratigraphic distribution of the agnathans in Paleozoic times. A, possible osteostracans (SMITH, 1991); B, possible thelodonts (SPJELDNAES, 1979); C, tesseraspids.

Répartition stratigraphique des Agnathes au Paléozoïque. A, Ostéostracés possibles; B, Thélodontes possibles; C, Tesseraspides.

mouth parts of hagfishes and conodonts suggests the later as possible relatives of the former. Recent studies have focused on these problems and the implications they have to phylogeny (KREJSA *et al.*, 1990a, b; SMITH & HALL, 1990; BRIGGS, 1992). The Silurian form *Jamoytius* might be related to the petromyzontids (BARDACK & ZANGERL, 1971; LUND & JANVIER, 1986), but it is *Hardistiella,* from the Lower Carboniferous, which is the earliest accepted record of a fossil lamprey.

ABBREVIATIONS

bo	branchial opening, *ouverture branchiale*;
bp	marginal (branchial) plate, *plaque marginale (branchiale)*;
bs	body scale, *écaille du corps*;
cn	nasal sac, *sac nasal*;
dr	dorsal crest, *crête dorsale*;
drs	dorsal rigde scale, *écaille de la crête dorsale*;
ds	dorsal shield, *bouclier dorsal*;
gr	dorsal shield and nasal bone (nb) groove, *bouclier dorsal et sillon pour l'os nasal (nb)*;
iol	infraorbital sensory line groove, *sillon sensoriel infra-orbitaire*;
k	branchial pit, *dépression branchiale*;
m	medio-ventral sensory groove, *sillon sensoriel ventro-médial*;
mds	dorso-medial sensory groove, *sillon sensoriel dorso-médial*;
n	nare, *narine*;
nb	nasal bone, *os nasal*;
or	orbit, *orbite*;
pi	pineal and parapineal depressions, *dépressions pinéale et parapinéale*;
s	sclerotic ossification, *ossification sclérotique*;
sbp	supramarginal plate, *plaque supra-marginale*;
sol	supraorbital sensory line groove, *ligne sensorielle supra-orbitaire*;
tz	transition zone between the dorsal shield and body scales, *zone de transition entre le bouclier dorsal et les écailles du corps*;
vlp	antero-ventrolateral projection of dorsal shield, *projection antéroventrale du bouclier dorsal*;
vs	ventral shield, *bouclier ventral*;
MHNC	Museo Historia Natural de Cochabamba;
MNHN	Muséum national d'Histoire naturelle de Paris;
YPFB PAL	Yacimientos Petrolera y Fiscales de Bolivia, Paleontological collection.

ORDOVICIAN VERTEBRATES

Leaving aside the question of the craniate affinities of the conodonts, recently proposed by BRIGGS (1992) and SANSOM *et al.* (1992), the earliest known vertebrates are from the Ordovician period. Records of Ordovician vertebrates consist of agnathan remains from the Stairway Sandstone in Australia (RITCHIE & GILBERT-TOMLINSON, 1977; RITCHIE, 1985), which are of Lower

Ordovician age (Early Llanvirn; Fig. 1). The vertebrate fauna from the Stairway Sandstone is represented by two agnathan species: *Arandaspis prionotolepis* and *Porophoraspis crenulata*. Some microremains, such as *Anatolepis* from Spitsbergen (BOCKELIE & FORTEY, 1976) which have been considered as vertebrate, are also known from the Upper Cambrian and Early Ordovician, but their vertebrate affinity is questionable (PEEL & HIGGINS, 1977).

The first described Ordovician vertebrates are from the Upper Ordovician in central North America (WALCOTT, 1892; DENISON, 1967; LEHTOLA, 1973; ELLIOTT, 1987; ØRVIG, 1989; ELLIOTT *et al.*, 1991). *Astraspis desiderata* and *Eriptychius americanus* are all of Caradoc age (Fig. 1). Other Ordovician vertebrates are known from North America such as *Astraspis* or *Pycnaspis splendens*, specifically differentiated by histologic characters of bony fragments, often of unknown anatomical position. DENISON (1967) described *E. oervigi* from Wyoming as having thicker dermal plates, with a more massive ornamentation than *E. americanus*. *E. leipnitzae* (SCHALLREUTER, 1983), is in fact an inarticulate brachiopod (BLIECK, 1992).

Astraspis is frequently recovered as isolated tesserae, ornamented with stellate tubercles. ELLIOTT (1987) reassessed *Astraspis* on the basis of new specimens collected in 1968, which had been misinterpreted by LEHTOLA (1983). ELLIOTT (1987) provided evidence for the presence of the dorsal shield, first thought to be a mass of poorly preserved scales, with part of the orbit and eight lateral branchial openings. The dorsal shield was previously known from the specimen recorded by WALCOTT (1892) and described by EASTMAN (1917: 238-239) in a footnote. It shows a shield made up of tesserae that bear small tubercles. ØRVIG (1958) identified the position of sensory line systems (see also STENSIÖ, 1964: 344-346) and pointed out the lack of a rostral region. The shield surface of *A. desiderata* shows a median crest (dr, Fig. 2B) and a pair of lateral crests along the edges of the shield. A group of elevated tubercles in anteromedian position might indicate the pineal organ (STENSIÖ, 1964). The remainder of the body is covered with triangle-shaped to rhombic scales. Contrary to ELLIOTT, after examination of a cast of the specimen I do not believe the caudal fin to be complete (Fig. 2B).

The second Harding Sandstone vertebrate, *Eriptychius americanus* (DENISON, 1967, Fig. 2), is generally found as isolated tesserae. These are ornamented with massive crests (ØRVIG, 1958, Fig. 5) and are easily distinguished from *Astraspis*.

Only one partially articulated specimen of *Eriptychius* is known to date (DENISON, 1967, Fig. 2). It shows the probable rostral part of a possible dorsal shield. SAWIN (1959) illustrated a group of scales of *Eriptychius*, similar to those described by DENISON (1967). They are thin and deep, rather than rhombic.

Arandaspis prionotolepis, from the Stairway Sandstone in Australia, as redescribed by RITCHIE (1985, Fig. 3A), has a dorsal and a ventral shield, separated by a slanting row of diamond-shaped platelets (Fig. 2A). RITCHIE (pers. comm.) found that each platelet bears a tiny hole and must thus represent branchial covers. The ornamentation is formed by rhombic tubercles. The dorsal shield shows parallel grooves interpreted as sensory lines. RITCHIE (1985) illustrates a paired pineal-parapineal opening. The rostral region is still not clear but one specimen shows a notch on the side of the dorsal shield that might represent the orbit (Fig. 2A). No bone is preserved in the Stairway Sandstone and therefore the histologic structure is unknown.

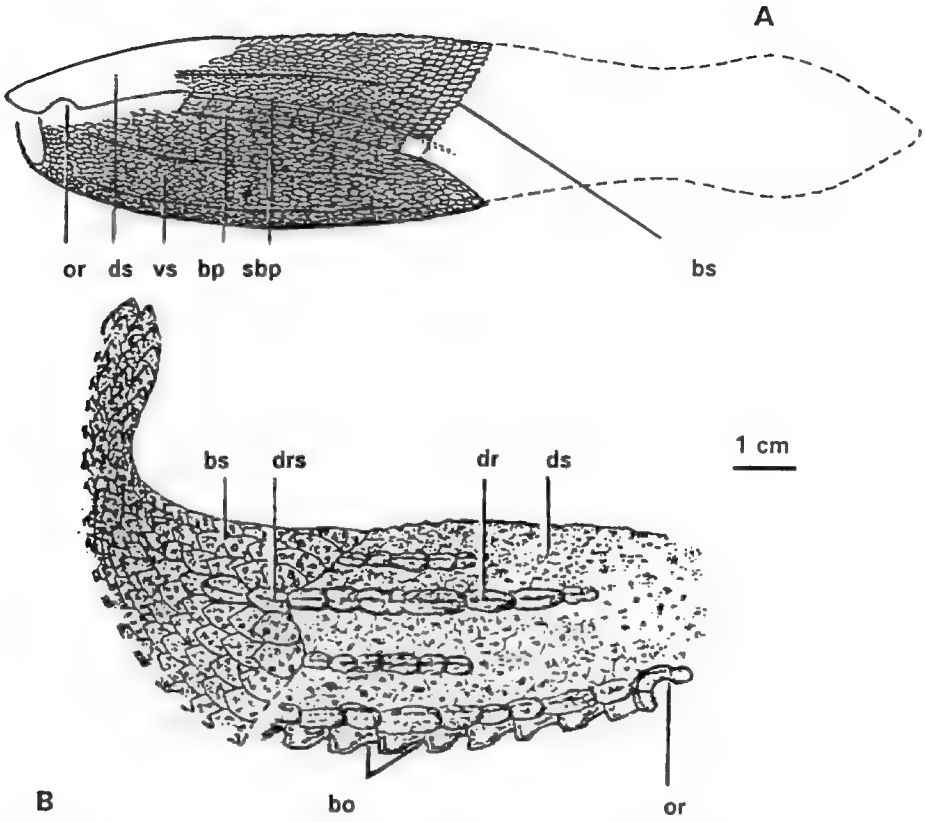

FIG. 2. — A, *Arandaspis prionotolepis*, reconstruction in right lateral view (modified from RITCHIE & GILBERT-TOMLINSON, 1977, Fig. 8; the anterior portion of the dorsal shield is reconstructed from RITCHIE, 1985 and unpublished material). B, *Astraspis desiderata*, reconstruction of an articulated specimen showing the orbit, eight branchial openings, body scales and incomplete caudal fin (modified from ELLIOTT, 1987, Fig. 3).

A. Arandaspis prionotolepis, *reconstitution en vue latérale droite (modifié d'après RITCHIE & GILBERT-TOMLINSON, 1977, fig. 8, la partie antérieure du bouclier dorsal est reconstituée d'après RITCHIE, 1985 et du matériel non publié). B,* Astraspis desiderata, *reconstitution d'un spécimen articulé, montrant l'orbite, huit ouvertures branchiales, les écailles du corps et la nageoire caudale incomplète (modifié d'après ELLIOTT, 1987, fig. 3).*

The body is covered by deep, thin scales with parallel ornamentation (Fig. 2A), arranged in chevrons on each side. No detail of the caudal fin is known.

The second species from the Stairway Sandstone, *Porophoraspis crenulata* is based on plate fragments which differ from the former species by the perforation of the diamond-shaped tubercles. These perforations, grade into scalloped margins of the tubercles, thereby making them resemble the oak leaf-shaped tubercules of various Silurian and Devonian heterostracans such as *Traquairaspis plana* and *Weigeltaspis alta* (RITCHIE & GILBERT-TOMLINSON, 1977).

The Australian genera were referred to the heterostracans on the basis of the presence of two large shields covering the cephalobranchial region and the shape of the ornamentation.

The latest discovered Ordovician vertebrate is *Sacabambaspis janvieri* (GAGNIER *et al.*, 1986), from the Anzaldo Formation of Bolivia (Llanvirn-Caradoc, Ordovician). It represents the first record of an Ordovician vertebrate showing most of the dermal skeleton (GAGNIER, 1987, 1988, 1989a, b, 1991, 1993; GAGNIER & BLIECK, 1992; BLIECK *et al.*, 1991; ELLIOTT *et al.*, 1991), and allows comparisons with other agnathans. More recently, *Andinaspis suarezorum* was described (GAGNIER, 1991) from supposedly Ordovician rocks of Bolivia. This form will not be discussed here, since its age remains uncertain.

DESCRIPTION OF *Sacabambaspis*

An extensive description of *S. janvieri* is provided in GAGNIER (1993a, b) but since it represents the best known Ordovician vertebrate, I shall give here a succinct description. Its average length (Fig. 3) is about 35 cm, of which the head shield represents more than a third. The shield is about 8 cm wide. The overall morphology is quite similar to that of *Arandaspis* from Australia, with two large bony units covering the head, and rows of lateral platelets. The body shape vaguely resembles that of a tadpole.

The head shield is formed by two large bone units composed of tiny platelets (tesserae) fused at the level of their basal layer. These platelets are roughly hexagonal in shape and have

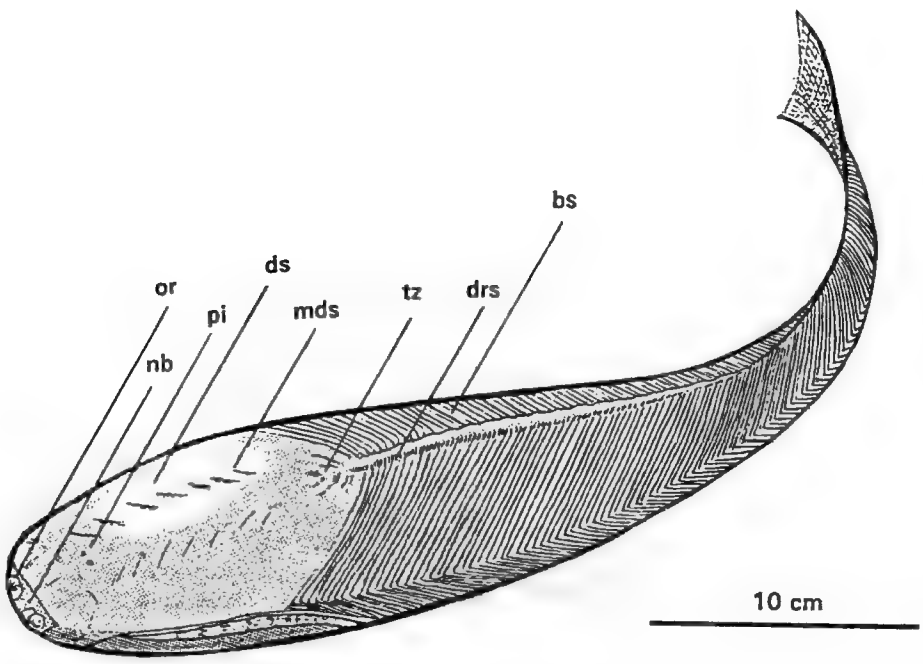

FIG. 3. — *Sacabambaspis janvieri*, reconstruction of an articulated specimen in right lateral view (modified from GAGNIER, 1989).
Sacabambaspis janvieri, *reconstitution d'un spécimen articulé en vue latérale droite (modifié d'après GAGNIER, 1989).*

an average size of 2 mm. Their external surface is ornamented with an oak leaf-shaped tubercle. The bone in the median part of the tesserae is enclosed by individual walls and the inner part is filled with spongious bone. No trace of discontinuity in the basal layer of the shield is visible, but it shows small nutrient foramina which may have served the irrigation of the bone.

The dermal bone tissue of *Sacabambaspis janvieri* is highly recrystalized, but nevertheless shows a mesostructure. It is made up of a thin laminar basal layer and a more important cancellous layer made up of polygonal chambers. Even if the bone of *Sacabambaspis* is highly recrystallized, there is no reason to believe that dentine or a hypermineralized enameloid tissue was covering the tubercles. At this structural level, certain vacuities are still present in the bone and are of the right size (2 to 5 µm) for cell spaces. The vacuities do not show any prolongation or smaller ramification. There is no indication that these vacuities are due to either recrystallisation, or a post-mortem decay such as fungic action.

The dorsal shield of the head (ds, Figs. 3, 4) has anterolateral projections which delimit an elliptical space containing the eyeballs and nostrils (or, Figs. 3, 4). These eyeballs are preserved as scleral and sclerotic (s, Fig. 4) ossifications. There is a median T-shaped bone (nb, Fig. 4), articulated with the dorsal shield and which separates two openings that may be interpreted as nostrils. The posterior end of the dorsal shield is transitional with the body scales. On the dorsal shield, there are paired depressions in the anterior median part of the shield (pi, Figs. 3, 4). Posterior to this paired depression, the tubercles of the dermal units are smaller and their orientation gives a false impression that there is a separate plate. This depression is interpreted as a paired pineal-parapineal aperture, because of the modified ornamentation of the surrounding platelets (GAGNIER, 1989a, b, 1991, 1993; GAGNIER & BLIECK, 1992).

The anterior part of the ventral shield is made up of square-shaped platelets aligned in rows to form the exoskeletal mouth apparatus. A little lump makes the transition between the mouth and the ventral shield. The ventral shield is deep and convex, and oval in shape in ventral view. It is strongly convex anteriorly and becomes flattened posteriorly, so that, in lateral view, it appears higher anteriorly and gently sloping posteriorly. Its posterior end is produced into a median, rounded, and convex lobe onto which are attached body scales forming a ventral median ridge.

On each side, the ventral shield is lined by a series of marginal plates (Fig. 3). There is a single dorsal one contacting with the dorsal shield on each side and a series of 18 to 20 smaller ones articulated between the supramarginal (sbp, Fig. 4) and the ventral shield on each side. They are diamond-shaped and some show a small posterior knob at midheight. They extend from approximately the level of the pineal openings to the posterior end of the ventral shield. They probably are covers for the external branchial openings.

The remainder of the body is covered with rows of thin, deep scales (bs, Fig. 3) ornamented with oak leaf-shaped tubercles similar to those of the shields, but arranged in parallel rows. There are four main scale rows covering the flanks, plus two small ones that form the dorsal (drs, Fig. 3) and ventral median scale ridges. The four main rows are arranged two-by-two in chevrons. There are more than a hundred scales along the axis of the chevrons. The scaled part of the body is about 25 cm long, of which 5 represent the tail. The ventral median ridge scales seem to end before the tail.

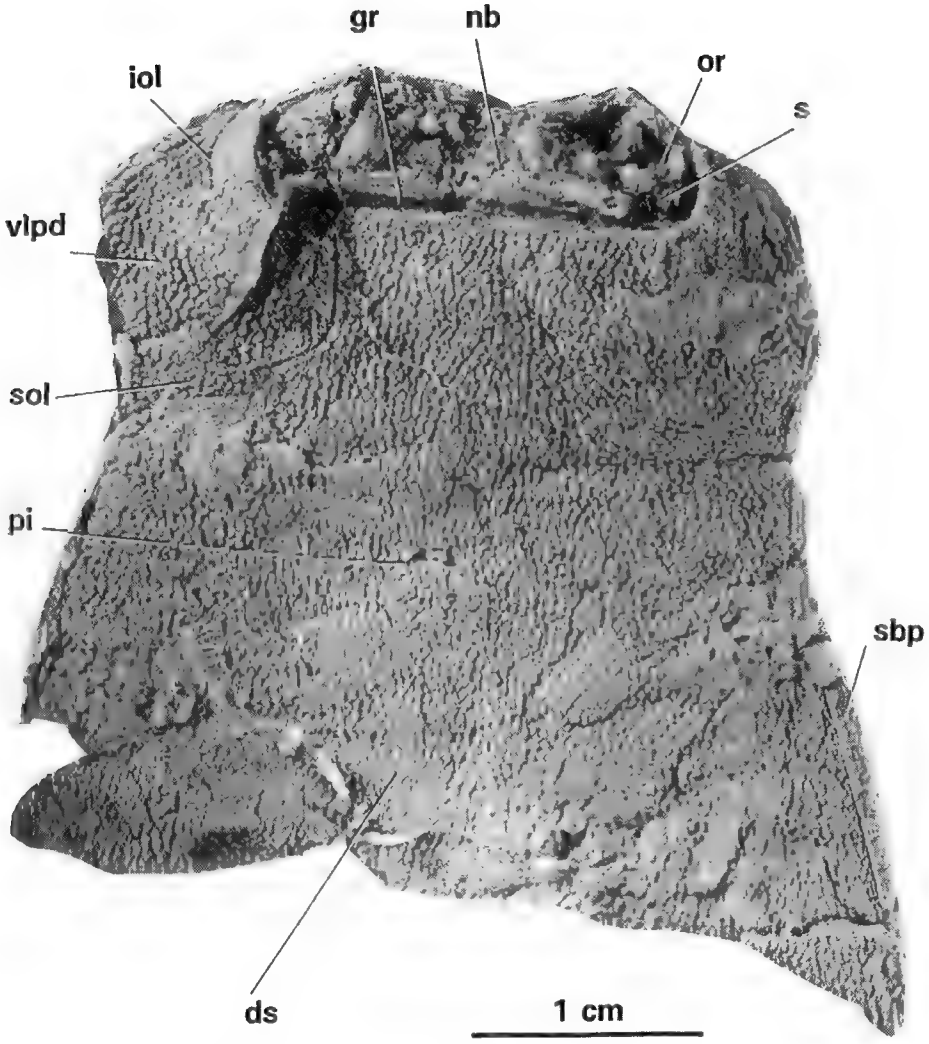

FIG. 4. — *Sacabambaspis janvieri*, cast of the natural mould in dorsal view, specimen MHNC 1005 b.
Sacabambaspis janvieri, *moulage du moule naturel en vue dorsale, spécimen MHNC 1005 b.*

The sensory line system consists of paired, longitudinal and transverse grooves. The dorsal shield also possesses two anterolaterally curved grooves that had been previously described on the holotype and specimen YPFB PAL-6206 (GAGNIER, 1987). There is also a discontinuous, paired, medial sensory line groove (mds, Fig. 3). On the ventral shield the sensory line pattern consists of a paired, medial, discontinuous line turning laterally near the mouth plates. In the lateral part of the shield is another discontinuous groove which runs posteriorly from the oral

region on the posterior two thirds of the shield and then turns ventromedially. A series of 18 to 20, laterally placed, transversal commissures is situated ventrally to each marginal plate row. There is a pair of ventrolateral lines on the body scales, running from the ventral shield on the two thirds of the body length. They are marked by a continuous and straight groove on the surface of the scales.

PHYLOGENETIC RELATIONSHIPS OF AGNATHANS

As generally accepted, craniates are characterized by the presence of a cranium, sensory capsules, and the neural crest and its derivatives (character 1). Vertebrates are characterized by such neontological features as the nervous regulation of the heart, or arcualia (characters 2, 3; see JANVIER, 1980: 381, 1981: 121). As FOREY (1984: 333) pointed out, the relationships of hagfishes and lampreys is not yet clear. I do not intend here to review the monophyly of the major agnathan groups. However, the relationships of the so called Ordovician heterostracans are reconsidered. I shall thus consider the taxa already defined and use their most recent definition, as proposed by FOREY (1984), JANVIER (1980, 1981, 1984), JANVIER & BLIECK (1979), and TURNER (1985, 1991).

BLIECK *et al.* (1991) revised the definition of heterostracans. It includes the distinction made by LANKESTER (1868-1870), who separated the Heterostraci from the Osteostraci by their histology. In the Heterostraci the bone is composed of aspidin, an acellular bone (LANKESTER's "bone without bone-lacunae"). The bone mesostructure consists of an internal lamellar layer, a thicker median cancellous layer, and an external layer of dentine ridges. A second character pointed out by LANKESTER (1870) is the presence of a single pair of dorsolateral branchial openings. FOREY (1984) mentioned a third heterostracan character: the presence of at least one median plate growing above and below the head. BLIECK *et al.* (1991) added a fourth heterostracan character: the lateral-line system enclosed in canals within the cancellous layer of the exoskeleton.

Recent studies on Ordovician vertebrates (BLIECK *et al.*, 1991; ELLIOTT, 1987; ELLIOTT *et al.*, 1991; GAGNIER, 1988, 1989, 1991; GAGNIER *et al.*, 1986; GAGNIER & BLIECK, 1992; ØRVIG, 1989; RITCHIE, 1985; RITCHIE & GILBERT-TOMLINSON, 1977), have shown that they are all more closely related to heterostracans than to any other craniate group. The main feature that unites the Ordovician vertebrates with heterostracans is the structure of the head armour, which consists of large median dorsal and ventral shields. ELLIOTT (1987), as previously noted, suggests that *Astraspis* should be excluded from heterostracans because of the presence of numerous pairs of branchial openings. ØRVIG (1989) arrived at the same conclusion on the basis of the histologic structure. GAGNIER (1988, 1989, 1991, 1993), GAGNIER & BLIECK (1992), BLIECK *et al.* (1991), ELLIOTT *et al.* (1991) also pointed out that *Sacabambaspis* and *Arandaspis* raised the same problem as to the presence of numerous pairs of branchial openings. The Ordovician vertebrates will be treated separetly, and the heterostracans will be represented in the analysis by the cyathaspids.

The characters used in the present phylogenetic analysis have been assessed as follows:

1. Neural crest and derivatives absent (0); present (1).

2. Neural arches absent (0); present (1).

3. Nervous regulation of heart absent (0); present (1).

4. General morphology. (0), head as broad as the body (burrowing habits at one stage of their development); (1), head dorsally flattened, ventrally bulged, and slightly larger than the body; (2), head dorsoventrally depressed, larger than the body.

REMARKS: Overall morphology is used here as an indicator of ecological trends. A similar elongated shape was pointed out by JANVIER (1981) in *Amphioxus*, myxinoids and petromyzontids. This shape is associated with a benthic or burrowing mode of life, at least during part of the life (larval stage of petromyzontid). The elongated morphology, with a head rounded in section and as broad as the body, associated with a benthic or burrowing mode of life could be considered as plesiomorphic.

Ordovician vertebrates and heterostracans have a head larger than the rest of the body, with the dorsal shield more or less flattened but the ventral shield bulged. In osteostracans and galeaspids it is the ventral part of the head that is flattened.

5. Head length/total length ratio. (0), 50% to 41%, stocky animal; (1), 40% to 31%; (2), less than 31%, animal elongated in shape.

REMARKS: The ratio of the head length to the total length gives an idea of the degree of stretching of the body. This ratio was obtained by measuring the current reconstructions. *Astraspis* have a ratio of about 50%, a value close to the one obtained for certain heterostracans, such as psammosteid. In pteraspidiform heterostracans this ratio is fluctuating around the 40%, but animals with a longer rostrum give an over-rated value. The cyathaspidiform value of 30% would be a better approximation.

Anaspids have a ratio of 25 to 30%, except for animals like *Euphanerops*, where it reaches up to 50%. This is linked to the development of numerous branchial pouches that could reach the anal region (ARSENAULT & JANVIER, 1991). Numerous branchial pouches is considered as a derived character in galeaspids (JANVIER, 1984: 349).

This ratio is about 17 to 25% in osteostracans and adult petromyzontids. In the former group, it reflects a shortening of the cranium (neurocranium + splanchnocranium). In petromyzontids where the splanchnocranium extends behind the neurocranium (rather than below as in osteostracans), it indicates an elongation of the body (compared to its larval stage).

6. Dermal bone absent (0); present (1).

REMARKS: The first question to answer is whether bone is present or absent in the common ancestor to all craniates. There seems to be a theoretical consensus on its presence, if we consider dermal bone as a derivative of the neural crest (ectomesenchyme), which is an apomorphy of the craniates (see SCHAEFFER, 1987). There is, however, no dermal bone in myxinoids, except if the conodonts are related to them. The conodonts have recently been shown as possibly possessing cellular bone and enameloid tissues (SANSOM *et al.*, 1992). Even if conodonts are not related to myxinoids, the presence of bone could be a derived character of the vertebrates (petromyzontids + gnathostomes) if it were present in petromyzontids, but it is not. However, some authors have produced analyses suggesting that the dermal bone might have been secondary lost in petromyzontids (JANVIER, 1981; HARDISTY, 1982; MAISEY, 1986). The rest of the vertebrates share the presence of a dermal skeleton.

As mentioned above, the comparison between lampreys (petromyzontids) and the other vertebrates is problematic because the majority of the characters of the fossil forms is of histological nature and concerns the dermal skeleton.

7. Bone cellular (0); acellular (aspidin) (1).

REMARKS: The primitive (DENISON, 1963; HALSTEAD, 1987) or derived (ØRVIG, 1958, 1967, 1989) state of the acellular bone tissue (aspidin) is still debated (see BLIECK, 1992). Histology does not provide any answer to this problem, but ØRVIG (1958), showed that acellular bone is more frequent in the latest forms of the vertebrate groups, such as acanthodians, actinopterygians, or osteostracans (ØRVIG, 1968), and this suggests that the primitive state would be cellular. In this scope, it is not surprising to find cellular bone in the Ordovician (BLIECK, 1992; DENISON, 1967; ØRVIG, 1965; SMITH, 1991; SPJELDNAES, 1979). This leads to the conclusion that acellular bone has a parallel history in the vertebrates as suggested by HALSTEAD (1982). The occurence of cellular bone as early as the Ordovician does not necessarily support the hypothesis of the presence of cellular bone in *Sacabambaspis*, but refutes primary objections.

8. Dentine absent (0); present (1).

REMARKS: *Sacabambaspis* displays a mesostructure, and the absence of a dentine layer recalls the heterostracan *Ctenaspis* (DENISON, 1964, Fig. 101C). Such an absence of dentine covering is not unique among the vertebrates. It was described in anaspids (GROSS, 1958) and galeaspids (JANVIER, 1990). In general, thelodont scales possess an orthodentine covering (KARATAJUTE-TALIMAA, 1978) or "multitubate" dentine (SMITH & HALL, 1990). Such dentine occurs in *Eriptychius* and heterostracans. Dentine is not very clear in *Astraspis*, but well-developed in the related genus *Pycnaspis*. ØRVIG (1989) notes that the North American Ordovician vertebrates are conform, in histologic structure, to heterostracans. I am inclined to agree that the orthodentine of *Eriptychius* resembles more that of the heterostracans than anything else (DENISON, 1967; HALSTEAD, 1987; ØRVIG, 1989; BLIECK, 1992).

In addition, *Sacabambaspis* has a bone mesostructure of cyathaspid type and *Astraspis* of pteraspid type. In *Eriptychius*, it is more of a psammosteid type (ØRVIG, 1989).

The polygonal tesserae of *Sacabambaspis* recall the tesserae of *Astraspis*, some heterostracans and even to some extent, osteostracans. This probably represents a primitive condition. In terms of shared characters, a basal layer that unites the entire shield into a large growing plate, is only present in *Sacabambaspis* and non-tessellate heterostracans. A cancellar acellular bone layer covered with dentine is shared by *Astraspis* (*Pycnaspis*), *Eriptychius* and heterostracans.

9. Ventral shield absent (0); or present (1).

REMARKS: The Ordovician vertebrates *Arandaspis* and *Sacabambaspis* possess two median shields, one dorsal and one ventral, as in heterostracans. Heterostracans possess additional plates, branchial, rostral, or cornual, that are unknown in the Ordovician vertebrates. *Astraspis* and *Eriptychius* might have possessed a ventral shield, but only the dorsal one is known. Material of the Wyoming Eriptychiidae could potentially relate that group to the heterostracans. A plate was interpreted as orbital by DENISON (1967) and branchio-cornual by ØRVIG (1989). These plates are only known in heterostracans.

10. Growth of the dermal shield cyclomorial (0); areal (synchronomorial) (1); or micromeric (2).

REMARKS: *Sacabambaspis* and *Arandaspis* share with the majority of heterostracans the presence of a macromeric cephalic shield. *Astraspis* possesses a mesomeric shield, as certain forms of tessellate heterostracans (*Tesseraspis* for example). *Eriptychius* also possesses a mesomeric shield, but its tesserae are of a different type (BRYANT, 1936; ØRVIG, 1958, 1967, 1989; DENISON, 1967; HALSTEAD, 1969, 1973a, b, 1974).

The relationships between the various agnathan forms are mainly dependent on hypotheses about the process of formation of the shield, *i.e.* whether it grows from a primitive tessellate stage to a completely fused shield, or from a large unit that evolves toward a fragmented stage. This question is still debated.

Historically, ROHON (1892) suggested that a macromeric stage could be a primitive state relatively to the large shields made up of small units. JAEKEL (1911) sees cyathaspids as an ideal primitive model from which all other forms could be derived. This point of view was discussed and followed by many authors such as STENSIÖ (1927), TARLO (1962, 1965), DENISON (1970), RITCHIE & GILBERT-TOMLINSON (1977: 365), following the same idea saw in the tessellate dermal skeleton of *Eriptychius* or *Astraspis* a condition derived from the dissociation of large, single-unit shields, like that of *Arandaspis*. They also suggested that the thelodont scales might have developed by a similar regression, from a macromeric stage.

Thelodonts differ from the other agnathans because of their scales, which are practically uniform all over the head and body. Their variations in scale pattern are limited to size and distribution. Contrary to the opinion of RITCHIE & GILBERT-TOMLINSON (1977), this uniformity suggests that it is primitive (ØRVIG, 1968, 1989; JANVIER, 1981). The Ordovician vertebrates from the Southern Hemisphere, *Arandaspis* and *Sacabambaspis*, share with heterostracans a macromeric state.

ØRVIG (1989: 430) pointed out the weakness in the reasoning which considers macromery as primitive. It rests on the assumption of a sudden appearance of a complete shield at the initial level of exoskeletal development. Such an armour (shield) certainly requires the interaction of a variety of mechanism and different histologic material. The complete sequence of events must have taken place by degrees of skeletal assimilation over a long period of time (ØRVIG, 1968: 374-388, 1975: 51-52, 1977: 69-72). The absence of dentine in some groups probably represents one particular degree of this sequence.

The idea of a primitive micromeric stage was defended by numerous authors (e.g. ØRVIG, 1951, 1989; STENSIÖ, 1958; TRAQUAIR, 1899, 1900; OBRUCHEV, 1944; TARLO, 1960; HALSTEAD, 1973a, b). STENSIÖ (1961, 1962, 1964) suggested a growth pattern that progressively organized cyclomorial units into larger unit or small plates in a synchronomorial way. He also suggested (1964) that the honeycomb-like middle layer of the exoskeleton in certain heterostracans, such as the Cyathaspidiformes, derived from the coalescence of cyclomorial units into a single macrostructure. In this case the dermal skeleton of *Astraspis* or *Eriptychius* represents, as HALSTEAD stated (1973b: 281), "the starting point for a subsequent evolution of the heterostracans carapace". Such a level of organization is also encountered in some heterostracans like *Tesseraspis*.

As to growth, ØRVIG (1989: 430) pointed out that if macromery is primitive, then large shields should not show any character considered as derived, such as concentric growth zone

or an association with separate tesserae (see also HALSTEAD, 1987: 344-345). Shields with concentric growth zones are well known in heterostracans (DENISON, 1964; WHITE, 1973; DINELEY & LOEFFLER, 1976; HALSTEAD, 1987) and present in *Sacabambaspis*, at least on the lateral margin of the shield (MHNC 1005 b, Fig. 4). The marginal plates 2 to 3 show rows of smaller tubercles along the margins than in the rest on the shield. It seems thus that macromery should not be retained as a primitive condition.

The armour of the Cyathaspidiformes (*sensu* "CA group", BLIECK *et al.*, 1991) is made up of dorsal and ventral shields, separated by a branchial plate. The cephalic shield of *Arandaspis* and *Sacabambaspis* is reminiscent of that of the Cyathaspidiformes.

BLIECK (1984) and BLIECK *et al.* (1991) think that the tesserae of such Ordovician taxa as *Astraspis* (Fig. 2B) or *Eriptychius* (DENISON, 1967, Fig. 2) are primitive, and that those of psammosteids are secondarily derived. Against this idea is the study by ØRVIG (1989) which highlights the similarity between the histology of the dermal bone of *Eriptychius* and psammosteids.

11. Differentiation of the dermal skeleton. No differentiation into cephalic and post-cephalic parts (0); mesomeric shield with post-cephalic tesseriform scales (1); mesomeric or macromeric shield with differentiated post-cephalic scales (2).

REMARKS: If we can reject the primitiveness of macromery, our present knowledge makes it difficult to decide which of the various types of mesomery and the micromery of the thelodonts could be primitive. Rather than theorising on the nature of the histologic development, I prefer to consider the skeletal macrostructural differentiation. ØRVIG (1989) pointed out the uniformity of the squamation of the thelodonts, where the only differences are the size and distribution patterns. Thelodonts do not show cephalic and postcephalic skeletal differentiation, contrary to the Ordovician vertebrates, heterostracans, anaspids and osteostracans. The tessellate heterostracan taxa, the cyathaspid *Athenaegis*, *Eriptychius* and *Astraspis* could be considered as showing an intermediate condition between non-differentiated and differentiated cephalic and postcephalic exoskeleton. The cyclomorial polygonal tesserae of the shield are all of the same size as the proximal trunk scales and grade into them (see STENSIÖ, 1964: 182, for the psammosteids; and ELLIOTT, 1987: 191, for *Astraspis desiderata*). If the dermal skeleton is originally mesomeric, then it is the scaled post-cephalic skeleton that is derived.

12. Exoskeletal mesostructure. Lamellar bone (0); bone with a lamellar base (1); bone without a lamellar base (2).

REMARKS: Like heterostracans, *Sacabambaspis* has a lamellar base covered by a spongy layer. It differs from the compact lamellar bone of anaspids or galeaspids. The histology of *Eriptychius* differs from that of *Astraspis* in that the mesostructure contains large ascending canals in the aspidin basal layer and elongated pulp canals beneath the dentine crests. However, there is an enameloid cap on the surface of certain crests (DENISON, 1967).

13. Perichondral bone, absent (0); present (1).

Perichondral bone in the endoskeleton occurs in osteostracans, galeaspids and the gnathostomes. This is regarded as a derived condition, relatively to hyaline cartilage alone.

14. Scales deep and narrow (0); rhombic (1); small, massive, micromeric (2).

REMARKS: Scale morphology is a character associated with the macrostructure of the dermal shield (see character 11). The thelodont scales resemble thus those of chondrichthyans in being of micromeric type. The scales of *Astraspis* are rhombic in shape (Fig. 2B), like these of *Tesseraspis* (WILLS, 1935) or *Athenaegis* (SOEHN & WILSON, 1990). The scales of *Astraspis* and *Eriptychius* seem to have an originally mesomeric structure and are considered as primitive by ØRVIG (1989). Pteraspid scales could be derived from an *Astraspis* type of scale, *i.e.* thick and rhombic in shape (WHITE, 1935; GROSS, 1963). Within the pteraspids there is an exception: *Doryaspis* which has deep, almost rectangle-shaped scales (STENSIÖ, 1968, Fig. 18A), but this is contradicted by BENDIX-ALMGREEN (1986: 95). This type of scales is of a cyathaspids type (KIAER & HEINTZ, 1935; DINELEY & LOEFFLER, 1976; BROAD & DINELEY, 1973; BLIECK & HEINTZ, 1983). Among the cyathaspids, *Athenaegis chatertoni* has rhombic scales.

Sacabambaspis and *Arandaspis* have very deep and narrow scales, like those of some anaspids and osteostracans. SAWIN (1959, Pl. 2: 3) illustrated deep and narrow scales in *Eriptychius*, thus different from those of DENISON (1967) which are more massive and rectangular in shape. Deep and narrow scales certainly represent a primitive type, as their arrangement matches the axial musculature (TRAQUAIR, 1905; SIMPSON, 1926; KIAER, 1924; PEARSON, 1980).

15. Shape of myosepta (myocommata). > -shaped (0); S -shaped (1).

REMARKS: If the scales, as suggested, reflect the arrangement of the myomeres, the trunk musculature most have been separated into two main parts which give the scales an anteriorly pointed chevron shape in *Sacabambaspis* and *Arandaspis*. SIMPSON (1926) supposed a possible concordance in the lateral musculature of anaspids and Cephalochordates. However, the concordance would be more accurate between *Sacabambaspis* and *Amphioxus*, where there is no ventral process. In anaspids, the position of ventral scales (character 15) clearly shows that the postbranchial myomeres had a ventral process. This ventral process is cranially directed, like in the osteostracans, petromyzontids or gnathostomes.

16. Caudal fin. Paddle-shaped (0); with horizontal chordal lobe (1); or strengthened with radials (2).

REMARKS: The caudal structure of the cephalochordates and myxinoids forms a paddle in which rays are not associated with the muscular system (regarded as a primitive condition for the craniates by JANVIER, 1981). Ordovician vertebrates do not have any fin other than the caudal. Heterostracans were believed to have a simple natatory paddle, like myxinoids, but the caudal fin of some heterostracans such as *Cardipeltis* or *Drepanaspis*, displays dermal ray-like lobes. Such "dermal rays" are also visible in *Athenaegis* (SOEHN & WILSON, 1990, Fig. 5C). A fin could have also existed in the "pteraspid indet. *Cosmaspis*?" of DENISON (1971, Fig. 9). SOEHN & WILSON (1990) suggested that it would be a functional convergence with bony fishes. However, JANVIER (1981: 144) argued that the presence of normal scale on the paddle and of dorsal and ventral ridge scales would not permit the presence of a fin with radials and radial muscles.

The homology of the caudal fin in the gnathostomes and osteostracans is based on the presence of radials which could have possessed a musculature (JANVIER, 1981). FOREY (1984) supported this interpretation in various fossil groups by the change in scale orientation on the caudal fin ("hinge line"). *Sacabambaspis janvieri* does not clearly show a change in the orientation of the scales in the caudal fin.

17. Caudal fin diphycercal (0); hypocercal (1); epicercal (heterocercal) (2).

REMARKS: Only the osteostracans and gnathostomes possess an epicercal (heterocercal) caudal fin, and the anaspids and thelodonts have a hypocercal caudal fin (*i.e.* the chordal lobe turns downwards). A divergent evolution may thus have a risen from the primitive diphycercal condition.

Diverse arguments have been raised about the structure of the caudal fin. *Sacabambaspis* and the petromyzontids both show a diphycercal tail. *Sacabambaspis* has large webs, dorsally and ventrally to the chordal lobe. Although the caudal fin of petromyzontids looks slightly hypocercal, FOREY (1984) pointed out that it possesses radials around the posterior tip of the notochord. The diphycercal tail of *Sacabambaspis* and petromyzontids may have had different histories of the lobe structure. Nevertheless, hypocercal and epicercal tails represent different trends in evolution, and there is no reason to consider one of them as primitive.

18. Anal fin absent (0); present (1).

REMARKS: An anal fin is known in the thelodonts, anaspids, and gnathostomes, where there is no median ventral scale ridge.

19. Ventral median preanal scale ridge scale present (0); absent (1).

20. Dorsal median scale ridge absent (0); present (1).

REMARKS: *Sacabambaspis*, like other Ordovician taxa, heterostracans and myxinoids which do not have any fin other that the caudal, have median, dorsal and ventral, preanal scale crest or skin ridge. These ridges are certainly plesiomorphic for the craniates, present in the outgroup, the cephalochordates.

A dorsal persists in osteostracans, although they possess one or two dorsal fins, and in anaspids.

21. Dorsal fin absent (0); present (1).

REMARKS: The petromyzontids and gnathostomes are the only groups to have dorsal and caudal fin radials associated with radial musculature (FOREY, 1984; HARDISTY, 1982; JANVIER, 1981; MAISEY, 1986). JANVIER (1981) suggests a possible relationship between the absence of other fins (paired and unpaired) and the presence of median ridge scales, but osteostracans and anaspids retain such scales. At least the dorsal ridge scales could persist along with the presence of dorsal fin. In the thelodonts, where median dorsal ridge scales are lacking (e.g. *Phlebolepis*), the dorsal fin does not show any character that suggests the presence of radials.

22. Pectoral fin absent (0); present in pectoral position (1); in epibranchial position (2).

REMARKS: Pectoral fins, when they exist in agnathans, are either in postbranchial position (anaspids) or in epibranchial position (osteostracans and thelodonts; M. WILSON, pers. comm.). They are associated with folds in ventrolateral position. The gnathostome pectoral fins are characterized by an endoskeletal structure and associated pectoral girdle musculature (*protractor pectoralis*; GREENWOOD & LAUDER, 1981). Osteostracans possess a *fenestra pectoralis* in the cephalic armour and their pectoral fins are narrow-based (STENSIÖ, 1927, 1968; JANVIER, 1978, 1981; JANVIER & BLIECK, 1979), but *Ateleaspis*, considered as primitive (JANVIER, 1984), has

broad-based paired fins, and tremataspids do not possess any. Homology is less than evident, the positive points being JANVIER's (1985) observations on the attachment area for the pectoral fin skeleton of a single specimen, and BELLES-ISLES (1987, 1989) black spots in the pectoral fin of *Alaspis macrotuberculata*, which could represent endoskeletal structures. Anaspids are known to possess dermal pectoral structure (spines) and fins with endoskeleton where also described (RITCHIE, 1964, 1968b, 1980, 1984). The flaps of thelodonts shows some similarity with the pectoral fins of skates, but is hardly comparable to a true pectoral fin. The sole common feature is that they are in a pectoral position.

23. Lateral fin fold present (0); absent (1).

REMARKS: *Sacabambaspis*, myxinoids, heterostracans, and possibly the petromyzontids [see, however, discussion in JANVIER (1981) suggesting that pectoral fins in lampreys could have been secondarily lost] might be considered as primitive because of the absence of lateral fin folds (see RITCHIE, 1964, 1968a, b, 1980, 1984; or JANVIER, 1981, 1987).

24. Horny teeth absent (0); present (1).

REMARKS: Myxinoids and petromyzontids share a simple mouth bearing horny teeth, which are unknown in other groups of craniates. Moreover, YALDEN (1985) considers the muscle-cartilage complex of the pseudolingual apparatus, as homologous in the myxinoids and petromyzontids. The presence of a lingual piston cartilage has never been clearly demontrated in other groups of craniates. It has no homologue in the gnathostomes. It was once supposed to be present in anaspids (*Pharyngolepis:* KIAER, 1924; SMITH, 1957; STENSIÖ, 1958, 1964). Later, RITCHIE (1964, 1980) revised the material used to support this idea and concluded that the structure referred to a "rasping tongue" was in fact a dermal bone and has nothing to do with the pseudolingual structure. A peculiar dumbell-shaped endoskeletal element was found in one specimen of *Sacabambaspis janvieri*, that may be associated with a pseudolingual apparatus. This remains, however, highly speculative.

25. Mouth functional structure. Annular cartilage (0); lower lips covered with scales, tesserae, or articulated plates disposed in a fan-like manner (1).

REMARKS: An annular cartilage has been claimed to be present in anaspids, this could be true if *Jamoytius* is regarded as an anaspid (RITCHIE, 1984). The annular cartilage could represent a unique shared character of petromyzontids and anaspids. The mouth is very poorly known in fossil agnathans except in heterostracans and osteostracans. The mouth is in a subterminal position in all agnathans except for the osteostracans and the galeaspids, where it is ventral, due to the shape of the animal.

It is only in the heterostracans that the mouth if fairly well described with its fan-shaped assemblage of more or less rectangular platelets (KIAER, 1928; WHITE, 1935; STENSIÖ, 1958, 1964; DENISON, 1960, 1961; JANVIER, 1981; SOEHN & WILSON, 1990, Fig. 6). The arrangement of the tesserae in the mouth region of *Sacabambaspis* recalls the condition in heterostracans. It represents a primitive condition from which the oral platelets of heterostracans may have evolved.

The mouth of the anaspids and thelodonts is poorly known, though surrounded by scales. In osteostracans (*Hirella*; HEINTZ, 1939), the lower lip, or postoral field, is composed of non-

organized tesserae. This condition is structurally – but probably not functionally – close to the tessellate "fan" of *Sacabambaspis*.

26. Branchial cover. No bony cover (0); bony cover present (1).

REMARKS: The specimen MHNC 1009 of *Sacabambaspis janvieri* shows a series of paired, transversal undulations on the dorsal shield placed in conjunction with the marginal plates. These undulations probably correspond to underlying branchial pouches (Fig. 5). The marginal plates can certainly be considered as branchial plates. *Arandaspis prionotolepis* also has the same marginal platelets (RITCHIE & GILBERT-TOMLINSON, 1977). The marginal and supramarginal plates in *Sacabambaspis* (Fig. 3) and *Arandaspis* (Fig. 2A) are thus a synapomorphy of arandaspids. No other agnathan group possesses ossified branchial covers. The osteostracan branchial openings, 8 to 10 in numbers, might have been protected by a small skin fold covered by dermal elements (HEINTZ, 1939; JANVIER, 1985), probably like in thelodonts (S. TURNER IN HOUT, 1990). In thelodonts, the dermal elements would be small scales, like on the body. The osteichthyans also possess an external branchial cover, the operculum, but the hyoidean cover (opercular) is certainly not homologous to the dermal covers of the agnathan, nor is the structural organization of the branchial system (MALLATT, 1984).

27. Number of pairs of branchial openings or arches. Between 5 and 7 (0); between 8 and 10 (1); more than 10 (2).

REMARKS: In anaspids, 8 to 18 pairs of openings are present as holes in a lateral plate and form a slanting row in the branchial region (STENSIÖ, 1964). Galeaspids could have to 24 pairs of branchial openings, but the galeaspids which are considered as primitive (JANVIER, 1984: 349) have between 7 and 10 pairs of branchial openings. Like in osteostracans, they are located on the margin of the oralobranchial cavity. Thelodonts have 8 to 10 pairs of independent branchial openings which seem to open on the ventral side of the animal (TURNER & IN HOUT, 1990). Thelodonts from the Canadian Arctic have their branchial openings arranged in a slanting row, like anaspids, lampreys, *Arandaspis* and *Sacabambaspis*. The Carboniferous lamprey *Hardistiella* does not seem to possess more than 6 pairs of branchial pouches, contrary to the modern forms which possess 7 (LUND & JANVIER, 1986). Myxinoids have from 6 to 15 pairs of branchial pouches (BRODAL & FÄNGE, 1963). Finally this number is fixed at 5 in the gnathostomes, except some elasmobranchs where it can reach 6 or 7, but this condition is considered as derived (MAISEY & WOLFRAM, 1984). In the majority of the agnathan groups, a large number of gill pouches is considered as derived, and a low number (5 to 7) plesiomorphic for the craniates. *Arandaspis* and *Sacabambaspis*, with their twenty pairs of branchial pouches are convergent with certain galeaspids and anaspids. Another possibility is that a large number is primitive and a low number deribed but homoplasic.

28. Morphology of branchial chambers. Pouch-shaped (0); transversally elongated (1).

REMARKS: The branchial pouches of myxinoids are in direct communications with the pharynx (AYERS & JACKSON, 1901), like in the cephalochordates, the larval of lampreys (Ammocetes) and the gnathostomes. The name Marsipobranchii, formerly used for the extant cylostomes refers to the pouch-like structure of their gill chambers, which differ from those of the gnathostomes. FOREY (1984: 338) mentioned that the branchial chambers of fossil agnathans

(heterostracans, osteostracans, galeaspids, thelodonts and here *Sacabambaspis*) are transversally stretched rather than forming small, rounded pouches, like in the myxinoids and petromyzontids. The gill lamellae are homologous in hagfishes, lampreys and the gnathostomes, but not the endoskeletal arches (JOLLIE, 1968; MALLATT, 1984).

An interpretation of the heterostracan branchial apparatus based on a gnathostomes model has been proposed by TARLO & WHITING (1965), HALSTEAD (1973a, b) and NOVITSKAYA (1983), but it is rejected by JANVIER (1981: 143). It is more simple to consider the branchial apparatus of the heterostracans as similar to that of osteostracans.

The myxinoids branchial apparatus is located far behind the braincase. The right and left pouches are disposed alternatively. This condition represents a parallel with the position of the lungs in snakes, where the secondarily elongated shape induces a shift of the internal organs.

Branchial openings arranged in slanting row have been suggested to be a derived condition shared by anaspids and lampreys (FOREY, 1984, Fig. 5). This character is linked with the forward

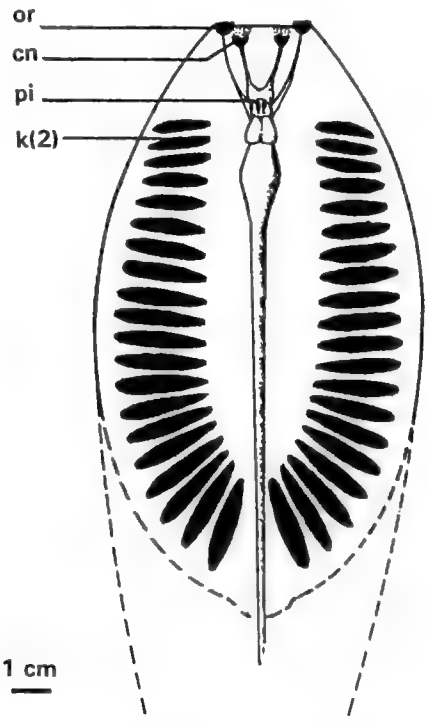

FIG. 5. — *Sacabambaspis janvieri*, hypothetical reconstruction in dorsal view, showing the approximate shape of the brain based on the size and position of eyeballs, pineal and parapineal fossae, the beginning of the dorsal shield crest, and the nasal bone suggesting the presence of two nasal sacs. The branchial fossae are reconstructed from the undulations observed on the dorsal shield of the specimen MHNC-1009 and the number and position of the marginal (branchial) plates.

Sacabambaspis janvieri, *reconstitution hypothétique en vue dorsale, montrant la forme approximative de l'encéphale sur la base de la taille et de la position des yeux, des fosses pinéale et parapinéale, de l'extension de la crête dorsale, du bouclier et de l'os nasal qui suggère la présence de deux sacs nasaux. Les fosses branchiales sont reconstituées à partir des ondulations observées sur le bouclier dorsal du spécimen MHNC-1009 et le nombre et la position des plaques marginales (branchiales).*

extention of the trunk musculature above and below the branchial apparatus. Also, the branchials opening series disposed in posteroventral slanting row in the anaspids, could have indicated the presence of an oesophagobranchial duct, like in lampreys (JANVIER, 1981).

29. Position of the external branchial openings. Lateral and arranged in a slanting row (0); ventral and arranged in a circle (1); dorsolateral (2).

REMARKS: Fossil agnathans show three tendencies for the position of the external branchial openings: a dorsolateral position (*Astraspis* and the heterostracans); a ventral position (osteostracans, galeaspids and some thelodonts), and arranged in a lateral, slanting row (*Arandaspis, Sacabambaspis*, petromyzontids, anaspids, and some thelodonts)

Heterostracans possess only one pair of dorsolateral branchial openings in the posterior part of the head shield (Fig. 6A). *Astraspis*, have a horizontal rows of 8 pairs (Fig. 6B), placed in a dorsolateral position on the head shield (ELLIOTT, 1987). Heterostracans also probably possessed

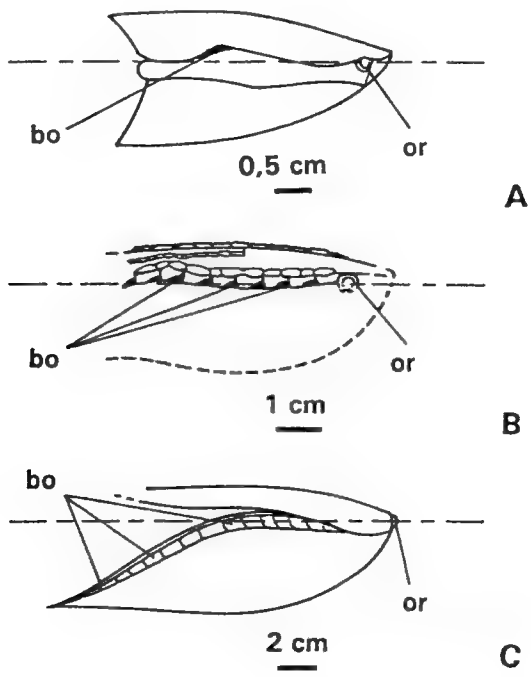

FIG. 6. — Right lateral view of the cephalic shield showing the position of the branchial openings. Dashed line (passing through the orbit) indicates the presumed base of the neurocranium. A, *Poraspis* representing heterostracans. B, *Astraspis* shares with heterostracans a reduced number and a dorsolateral position of the branchial openings. C, *Sacabambaspis janvieri* displays quite a different condition, with the large number of external branchial openings arranged in slanting row.

Vue latérale droite du bouclier céphalique montrant la position des ouvertures branchiales. La ligne en pointillé indique le niveau présumé de la base du neurocrâne. A, Poraspis, *représentant les Hétérostracés. B,* Astraspis *partage avec les hétérostracés un nombre réduit et une position dorso-latérale des ouvertures branchiales. C,* Sacabambaspis janvieri *présente une structure bien différente, avec un grand nombre d'ouvertures branchiales disposées en rangée oblique.*

8 pairs of branchial arches as suggested by undulation on the natural mould of certain forms such as *Seretaspis* (STENSIÖ, 1958, Fig. 204) or *Anglaspis*. The low number of branchial arches and the dorsolateral position of the external branchial openings on the head shield seem to be shared by *Astraspis* and heterostracans. A morphocline is possible from a condition like that in *Sacabambaspis*, where the branchial openings are in slanting row (Fig. 6C) to a dorsolateral position, like in *Astraspis* and heterostracans. The reduction to a single pair of common external branchial openings is unique to heterostracans.

30. Number of external branchial openings equal to that of branchial pouches (0); or single common external branchial opening (1).

REMARKS: A single pair of external branchial openings is regarded as a unique heterostracan character (LANKESTER, 1870; JANVIER & BLIECK, 1979; JANVIER, 1981; FOREY, 1984). Such a condition is not unique in craniate history because it also occurs in *Myxine*, osteichthyans and holocephalans. In myxinoids, the number of the external branchial openings varies from a single one to 15 pairs. The embryology of the *Myxine* (HOLMGREN, 1946) shows that the presence of multiples external branchial openings is plesiomorphic for the group. So, the acquisition of a single pair must be a parallelism, contrary to what was suggested by STENSIÖ (1927, 1958, 1964, 1968) or JARVIK (1965).

31. Nasal sac single and bilobate in shape (0), paired (1).

REMARKS: The development of the olfactory organ was a subject of controversy. In this controversy, two different questions are to be considered: the condition of the nostrils and the structure of the olfactory organ proper. Monorhiny and Diplorhiny where often confused by the interpretations made on the basis of the nostrils. One of the main point is to know whether the primitive condition of the olfactory organ is paired, because of the basic bilateral symmetry of the craniates, or unpaired because of the location of the organ in the terminal segment. The Kölliker organ of the cephalochordates fails to prove to have any homology with the craniate olfactory organ. Thus, there is no possible outgroup comparison. Two patterns are known in extant craniates: a single, unpaired, bilobate capsule (myxinoids) which can be divided by a median septum (petromyzontids); or two independent capsule in the gnathostomes. The myxinoids and petromyzontids pattern may be the consequence of an overall elongated shape, but embryology is inconclusive and, therefore, it may also be considered as a shared derived condition termed as "monorhiny".

The anterior position of two nostrils in heterostracans, supposed by NOVITSKAYA (1975), refutes the hypothesis of a prenasal sinus, like in myxinoids, as suggested by STENSIÖ (1927, 1968) and JANVIER (1975b, 1981).

The impression of two olfactory tracts on the internal surface of dorsal shield in heterostracans leads some authors (HALSTEAD, 1973a, b; NOVITSKAYA, 1975) to the conclusion of the presence of two independent olfactory capsules. Opponents argue that a single, median nostril is known in heterostracans. From that point, the argumentation becomes confused in assimilating two characters: the nostrils and the olfactory organs. In *Sacabambaspis* the paired nostril is shown by the anterior T-shaped bone forming a dermal septum (Fig. 4). It suggests the presence of two separate nasal capsules (Fig. 5).

32. Nostrils. Monorhiny (single median opening) (0); diplorhiny (paired of nostrils) (1).

33. Nasohypophysial duct absent (0); present (1).

REMARKS: Galeaspids have a large median dorsal opening that recall the nasohypophysial opening of osteostracans, but morphologically and structurally different, as it communicates ventrally with the oralobranchial chamber. This opening has been interpreted as a nasopharyngeal duct [exhalent by BELLES-ISLES (1986) and inhalent by JANVIER (1981, 1984)]. Recently, WANG (1991a, b) described two independent olfactory capsules in the anterior part of a galeaspid skull. This discovery shows the coexistence of paired olfactory capsules and a single median dorsal opening. The galeaspids thus display a perfectly intermediate condition between diplorhiny and monorhiny. Anaspids possess a median dorsal opening which looks like a nasohypophyseal opening, but the internal structure of these forms is still unknown. On the contrary, osteostracans have an endoskeleton which shows that the median dorsal opening is a blind nasohypophyseal opening, much like that of petromyzontids (KIAER, 1924; STENSIÖ, 1927, 1964, 1968; WÄNGSJÖ, 1952; JANVIER, 1975b, 1981; FOREY, 1984). A blind nasohypophysial opening, that does not communicate with the pharynx is restricted to the petromyzontids and osteostracans.

34. Position of nostrils anterior (0); dorsal (1).

REMARKS: The development of lamprey shows a nasohypophysial opening which is first ventral, in communication with a bilobate capsule, and then migrates dorsally. Thus, it is reasonable to accept that a ventral or terminal opening, associated with two olfactory sacs is a primitive condition for the vertebrates. Secondary fusion of the olfactory sacs is suggested by the presence of two olfactory nerves.

35. Nasopharyngeal duct present (0) or absent (1).

REMARKS: JANVIER (1981, 1984) considered the nasopharyngeal duct (*i.e.* communicating with the pharynx) as primitive for the craniates, since it is the condition in myxinoids. Such an inhalent duct is present in galeaspids. The condition in heterostracans and thelodonts is unknown, despite JANVIER's (1981) claim that these taxa possessed a nasopharyngeal duct.

36. Sensory lines absent (0), present but superficial (1), or deeply sunken in the dermis (2).

REMARKS: Among extant craniates, ony the petromyzontids and gnathostomes possess a sensory line system on the head. The condition in myxinoids is unclear. KUPFFER (1900) and AYERS & WORTHINGTON (1907) showed that grooves on the head of *Bdellostoma* originated from the same embryonic territory as the lateral line system, but failed to demonstrate a connection with the sensory system. FERNHOLM (1985) considered that these lines most probably correspond to the sensory lines in *Eptatretus*.

Sacabambaspis (Fig. 3), osteostracans, galeaspids, and the gnathostomes possess a single pair of longitudinal dorsal sensory lines on the head shield. Heterostracans always have two pairs of longitudinal dorsal sensory lines, which might represent an autapomorphy.

37. Ventral sensory line absent (0), present as a single pair (1), or present as two pairs (2)

38. Distribution of trunk lateral lines. Single pair of horizontal segments, never reaching the caudal fin (0); three pairs of horizontal segments, never reaching the caudal fin (1); three pairs of horizontal segments of which one reaches the caudal fin (2).

REMARKS: Thelodonts and certain acanthodians show three segments of the lateral line system on the trunk, of which the middle one reaches the caudal fin. The homology of the trunk segments is uncertain. Nevertheless, the thelodonts show a typical gnathostome pattern, contrary to other agnathans which possess a pair of ventral lines that do not extend to the caudal fin.

39. Trunk lateral lines absent (0); present as free neuromasts in grooves (1); or present as canals (2).

REMARKS: the trunk sensory lines of the gnathostomes are enclosed in modified scales (AYERS & WORTHINGTON, 1907). Groove-like sensory lines are present in *Sacabambaspis* and *Arandaspis*. It was previously recorded from anaspids, galeaspids, and some heterostracans such as the amphiaspids. Certain authors (PEHRSON, 1922; STENSIÖ, 1921) suggest that sensory line probably originate from induction of lateral components of the dermal skeleton. Since the neuromasts originate from placodes, thus, sensory lines in grooves could be easily regarded as primitive and those enclosed in canals as derived. Thus the sensory groove in *Sacabambaspis* could be regarded as a starting point from which could independently evolve the gnathostome and heterostracan trunk lines.

40. Scleral (perichondral) ossification. Absent (0); present in eyeball (1).

REMARKS: The anterior position of the eye of *Sacabambaspis* (Figs. 3-5) certainly represents an autapomorphy because it is unknown in all other craniates, even in the early embryonic development. In all other agnathans, the eyes are in lateral position except in galeaspids and osteostracans where they are in a dorsal position due to the shape of the animal. The primitive galeaspids, such as *Hanyangaspis*, have their eyes in lateral position rather than dorsal, as in the supposedly more derived. This suggests a parallel evolution in galeaspids and osteostracans. ELLIOTT (1987) described a circumorbital bone in *Astraspis* (Fig. 2B). Such a bone is known in the Cyathaspidiformes, *Athenaegis chatertoni* (SOEHN & WILSON, 1990, Figs. 2F, 3, 4, 5E). A perichondrally ossified sclera is known only in osteostracans and the gnathostomes (placoderms). It may, however, exist also in *Sacabambaspis*

41. Sclerotic (dermal) ossification. Absent (0); present (1).

REMARKS: A dermal sclerotic ossification is known in *Sacabambaspis*, osteostracans, and the gnathostomes.

42. Oculomotor musculature absent, with conical eyeball (0); present (1).

REMARKS: Myxinoid eyes have classically be considered as primitive (STENSIÖ, 1927), simple, without crystalline and conical in shape. The heterostracan eyes have been compared with those of myxinoid because of the impression left in the dorsal shield of the former. This was to support an interrelationship (JANVIER, 1975a) and implicitly refute the presence of an oculomotor musculature. The simple myxinoid eye structure could also be due to degeneracy, in turn linked with their mode of life.

The eyes of lampreys have an extrinsic musculature attached to the orbital cavity (HARDISTY, 1982), like in the gnathostomes. The eyeball of *Sacabambaspis* with both scleral and sclerotic

ossifications, suggest the existence of an oculomotor musculature. The oculomotor musculature seems to be more widespread in vertebrates than previously thought.

43. Corneal musculature. Absent (0); present (1)

REMARKS: A corneal musculature has been also suggested to exist in anaspids (JANVIER, 1981), like in lampreys, due to scale arrangement around the orbit. The corneal musculature is innervated by the oculomotor nerve (III) and seems to be homologous to the oculomotor musculature (NICOL, 1989). The inferior rectus muscle is innervated by the abducens nerve (VI) in lampreys, and by the oculomotor nerve (III) in the gnathostomes (ROVAINEN 1979). This muscle may not be homologous in the two groups.

44. Pineal and parapineal organs in a single median cavity (0), or side by side (1).

REMARKS: In vertebrates, the pineal and parapineal organs are respectively in relation with the right and left habenula, suggesting a primitive symmetry. However, BJERRING (1975) suggested a possible homology of the pineal with the median eye of larval ascidian tunicates, which develops in relation with the anterior cerebral vesicle. BJERRING's suggestion thus implies that the pineal organ was primitively single and median. Even if there is no homology between the median eye of the tunicates and the pineal organs, developmental studies fail in linking functionally the pineal and parapineal organs (WINGSTRAND, 1966), and thus gives no support to an original symmetry.

Some heterostracans, osteostracans, galeaspids, anaspids have only one pineal foramen. *Arandaspis* (RITCHIE, 1985) shares with *Sacabambaspis* a double depression, pineal and parapineal, where the two organs are side by side (Figs. 3-5). This character is not shared with any other agnathan and is considered here as a synapomorphy.

45. Nerves IX and X issuing behind the braincase (0); from the braincase (1).

REMARKS: This character, taken from FOREY (1984), concerns the position of the two last cranial nerves, inside or outside the brain case. In the galeaspids, osteostracans, and gnathostomes the nerves IX and X are issued from the braincase, whereas they are issued behind the braincase in petromyzontids and myxinoids.

CONCLUSIONS

THE RELATIONSHIPS OF THE ORDOVICIAN VERTEBRATES

Character analysis using PAUP software 2.4.1 for IBM compatible (SWOFFORD, 1985) was performed. A single matrix was built, including different taxonomic levels. Cyathaspids were used to code for the Heterostraci. Cephalochordates were used as an outgroup. The character matrix shown in table 1 was also simplified. A first analysis was produced, with cyathaspids representing the heterostracans, and *Eriptychius* being removed. The 12 taxa and 45 unordered characters left gave a single tree of 102 steps, with a consistency index of 0.578. In a second analysis anaspids, galeaspids, osteostracans, thelodonts, and chondrichthyans were removed as well as all the characters that became useless.

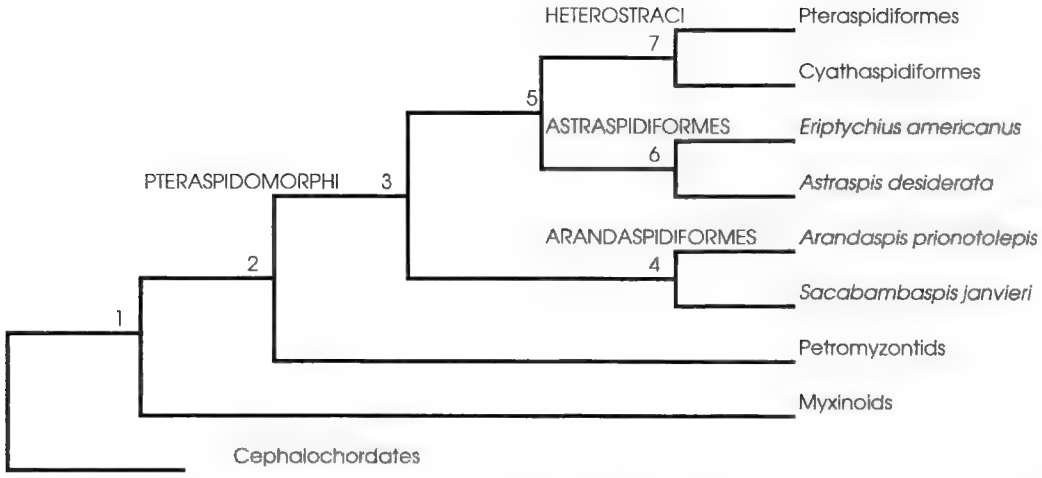

FIG. 7. — Hypothesis of the phylogenetic relationships in the Pteraspidomorphi. For node 1 and 2, the reader is referred to figure 8. 3, median dorsal and ventral growing plates covering head; dermal bone with lamellar base and spongy middle layer; two anterior nostrils (diplorhiny). 4, more than 10 pairs of branchial arches with individual branchial covers; pineal and parapineal organs placed side by side. 5, tesseriform postcephalic scales and rhombic body scales; branchial openings in dorsolateral position; dermal bone covered with dentine. 6, animal short and robust, with a mesomeric shield; acellular dermal bone with basal layer non-lamellar but cancellar or pierced by pulp cavity openings; bone covered with superficial dentine layer. 7, single pair of branchial openings.

Hypothèse de relations de parenté au sein des Pteraspidomorphi. Pour les noeuds 1 et 2, se reporter à la figure 8. 3, plaques médianes dorsale et ventrale croissantes et couvrant la tête, os dermique à couche basale lamellaire et couche moyenne spongieuse; deux narines antérieures (diplorhinie). 4, plus de 10 paires d'arcs branchiaux avec opercules individuels; organes pinéal et parapinéal situés côte-à-côte. 5, écailles postcéphaliques tessériformes et écailles du corps rhombiques; ouvertures branchiales en position dorsolatérale; os dermique couvert de dentine. 6, animal trappu, avec un bouclier mésomérique; os dermique acellulaire à couche basale non lamellaire mais cancellaire ou percée de foramens pour les cavités pulpaires. 7, une seule paire d'ouvertures branchiales.

Using previous phylogenetic studies by JANVIER & BLIECK (1979), JANVIER (1981, 1984), FOREY (1984), ELLIOTT (1987) and WANG (1991b), GAGNIER (1987, 1989), GAGNIER *et al.* (1986), and considerations of Ordovician vertebrates by BLIECK *et al.* (1991) and ELLIOTT *et al.* (1991), GAGNIER & BLIECK (1992) suggested a pattern of interrelationships in which *Sacabambaspis* shares only one synapomorphy with heterostracans: the large ventral and dorsal shields covering the head. It was also pointed out that the sculpture of the shield ornamentation shows a gradation from *Arandaspis* to *Porophoraspis* and *Sacabambaspis*, starting from diamond-shaped tubercles which would become sculptured into an oak leaf-shaped tubercle (G.C. YOUNG, pers. comm.). The elongated tubercles of *Eriptychius* seem closer to this pattern than the stellate ornamentation of *Astraspis*. *Sacabambaspis* shares with *Arandaspis* the branchial openings arranged in a slanting row, each one being covered by a platelet, whereas these seem to form a horizontal row in *Astraspis* (ELLIOTT, 1987). The double pineal depression in *Sacabambaspis* and *Arandaspis* is not present in *Astraspis*. The elongated shape of the body scales is also known in *Eriptychius* (SAWIN, 1959, plate 2: 3), but these are closer to the rhombic scales of *Astraspis* (ELLIOTT, 1987). These considerations supposed that *Sacabambaspis* would be the sister group of *Astraspis* and heterostracans (Fig. 7).

The phylogenetic analysis of the craniates characters highlights the close relationship between Ordovician vertebrates and the heterostracans. The Northern Hemisphere Ordovician taxon are the sister-group (Astraspidiformes) of heterostracans and the Southern Hemisphere Ordovician taxon (Arandaspidiformes) is the sister-group of the former assemblage, *i.e.* heterostracans plus Astraspidiformes. I suggest to name the ensemble of Arandaspidiformes, Astraspidiformes and Heterostraci, as the Pteraspidomorphi.

This analysis leads to the following definition of the higher taxa.

Class PTERASPIDOMORPHI Goodrich, 1909

The Pteraspidomorphi include the Ordovician vertebrates and heterostracans. It would thus include the Arandaspidiformes, Astraspidiformes, Cyathaspidiformes, Pteraspidiformes and probably various tessellated taxa. These four major groups share the presence of an armour made of two large median plates, one dorsal and one ventral (character 9; one of the characters in: BLIECK *et al.*, 1991; FOREY, 1984; JANVIER, 1981; JANVIER & BLIECK, 1979). These plates have a concentric growth (character 10). The mouth apparatus is made up of an inferior lip covered with scales, tesserae or mobile and articulated plates arranged in a fan-shaped pattern (character 25), and a diplorhinal state (characters 31, 32). This new definition may change when more is known of the Astraspidiformes.

The Astraspidiformes and Heterostraci (Cyathaspidiformes and Pteraspidiformes) are united principally by the shape of the scales (character 14), a tessellate armour (characters 10, 11), and the histologic structure, made up of acellular bone with a similar structure in Astraspidiformes and certain psammosteids (ØRVIG, 1989). The rhombic scale shape and the tessellate structure of the armour existed in such Cyathaspidiformes as *Athenaegis*.

In arandaspidiforms and cyathaspidiforms, the middle layer is divided into small chambers and the plates have concentric growth (character 10).

Order ARANDASPIDIFORMES Ritchie and Gilbert-Tomlinsson, 1977

The Ordovician vertebrates, *Arandaspis* and *Sacabambaspis* form the family Arandaspididae in their own order, the Arandaspidiformes. They are characterized by a bony branchial cover (marginal plate) on each external branchial opening (character 26) and a long and narrow supramarginal plate. Trunk scales are deep and slender (character 14), and a ventral sensory line runs on them (character 35). Pineal and parapineal organs are placed side by side (character 44).

Beside the ornamentation of their dermal skeleton, *Arandaspis* and *Sacabambaspis*, differ by the division of the supramarginal plate. There is a single supramarginal plate in *Sacabambaspis* rather than individual platelets dorsally to each marginal plate in *Arandaspis*. *Porophoraspis* is provisionally included here because of the ornamentation and the presence of large plates.

The Arandaspidiformes share with the Heterostraci (Fig. 7) the presence of median plates with concentric growth, covering the head dorsally and ventrally (characters 9, 10), and a diplorhinal condition (character 32).

Superorder ASTRASPIDA Stensiö, 1958 (= Berg, 1937)

The Astraspidiformes and Heterostraci (Cyathaspidiformes and Pteraspidiformes) share the presence of dentinous tissue (character 8) and the bone made up of aspidin (character 7). They also share a low number of gill chambers (character 27), branchial openings, and their dorsolateral position (character 29; Fig. 6). Other characters may support this grouping, but are poorly documented, such as the possible reduction of the eye musculature (character 42), or the reduction of the caudal fin to a simple paddle (character 16). The North American Ordovician vertebrates share more derived characters with the Heterostraci than arandaspids.

Order ASTRASPIDIFORMES Berg, 1937

The Astraspidiformes are known essentially by the family Astraspididae which comprises the genera *Astraspis* and *Pycnaspis* (HALSTEAD, 1973b). For convenience, the Eriptychiidae are here included in the same order, Astraspidiformes. The name Astraspidiformes has been used by HALSTEAD (1973b), but no definition was given. This author placed *Eriptychius* in its own order that contains the Eripychiida and Tesseraspida. I do not retain these taxa, owing to the lack of data on these groups. The Astraspidiformes are characterized by a tessellate cephalic shield (characters 10, 11) and by the mesostructure of the dermal bone, with a non-lamellar base that could either be cancellar or notched by pulp cavities, and covered with a superficial hypermineralized tissue (character 12).

Certain tessellate taxa classically placed in the Heterostraci seem to share some characters with the Astraspidiformes. The synchronomorial growth of the plates and the type of ornamentation that form the dorsal shield (tessellate structure, characters 10, 11) suggest a relationship between *Eriptychius* and *Tesseraspis* (OBRUCHEV, 1964; HALSTEAD, 1973b). The two dorsal and lateral crests of *Tesseraspis* might represent a shared character with *Astraspis*.

Order HETEROSTRACI Lankester, 1868-70

The Heterostraci include two major taxa, the Cyathaspidiformes and Pteraspidiformes. They form a monophyletic group, characterized by a single pair of branchial openings in dorsolateral position (character 30).

Suborder CYATHASPIDIFORMES Berg, 1937

The Cyathaspidiformes (*sensu* "CA group" in BLIECK *et al.*, 1991) include cyathaspids and amphiaspids, and are defined by an armour made up of median dorsal and ventral plates, separated by branchial plates (fused in amphiaspids); the lateral-line system is composed of two pairs of longitudinal lines, with at least three transverse commissures on the dorsal shield. The pineal branches of supraorbital canal do not join to form a V; the dentine crests are longitudinal and laterally crenulate; the body scales are deep and rectangular in shape (BLIECK *et al.*, 1991).

Suborder PTERASPIDIFORMES Goodrich, 1909

The Pteraspidiformes (*sensu* "APP group" BLIECK *et al.* 1991), including anchipteraspids, pteraspids, and psammosteids, are defined by cephalic armour formed by dorsal and ventral median plates, pineal and rostral plates, a pair of orbital plates (two pairs in psammosteids), and branchial and cornual plates (branchiocornual in anchipteraspids); the sensory-line system of the dorsal shield is the same as in Cyathaspidiformes, except for the pineal segment, which forms a V-shaped commissure; the ornamentation consists of concentric ridges with serrated margins; the body scales are thick and rhombic in shape (BLIECK *et al.*, 1991).

THE RELATIONSHIPS OF THE PTERASPIDOMORPHI

Authors like STENSIÖ (1927, 1964) or JANVIER (1975a, b) proposed a relationship between myxinoids and the Pteraspidomorphi. Morphological characters of *Sacabambaspis janvieri*, such as those of the eyes, nostrils, dermal skeleton, lateral-line system or trunk musculature refute this hypothesis.

In the present hypothesis (Fig. 8), petromyzontids are the most primitive vertebrates. Beside the absence of a dermal skeleton (characters 6-12, 14, 26), the petromyzontids and myxinoids have a branchial apparatus with individualized pouches in relation with the pharynx (characters 28, 35), a mouth armed with horny teeth, and a pseudolingual apparatus like (character 24, 25). These characters were considered as homologues by YALDEN (1985), which used them in the justification of the monophyly of the cyclostomes. However, even if the homology of these characters is not disputed, they are here regarded as craniate characters, and the cyclostomes remain paraphyletic in this analysis.

The present analysis suggests that the dermal bone is a derived character within the vertebrates. This is not surprising since this study is largely based on fossils. Placing petromyzontids as the most primitive vertebrates poses certain problems in particular with the median fins. The plesiomorphic state would be the lack of median fins and the presence of a median dorsal scale ridge. One of the solution is, as suggested by JANVIER (1981), to consider the absence of dermal skeleton and anal fin as secondary and thus to put the petromyzontids higher in the classification.

The name Myopterygii (JANVIER, 1978) may be considered as synonym of Vertebrata. The presence of two individualized nasal sacs (character 31) and the retention of a median external opening (character 32) in galeaspids legitimates the assumption that Diplorhiny is derived. It should be noted that the presence of two nasal sacs is attested only in animals with a broad head (character 4, 31). Two individual nasal sacs may be primitive for the vertebrates as suggested by the double olfactory tractus in petromyzontids.

The presumed relationship between galeaspids and osteostracans (HALSTEAD, 1982; JANVIER & BLIECK, 1979; JANVIER, 1984), seems to be due, in a large part, to homoplasies in the morphology of these animals: the dorsoventral flattening, the mouth in a ventral position (character 25), the branchial openings arranged into a ventral circle (character 29), and the trend toward a dorsalisation of the eyes and nasal opening (character 34). The histologic structure of the bone in galeaspids and the morphology of the olfactory system suggest that galeaspids are primitive bony vertebrates.

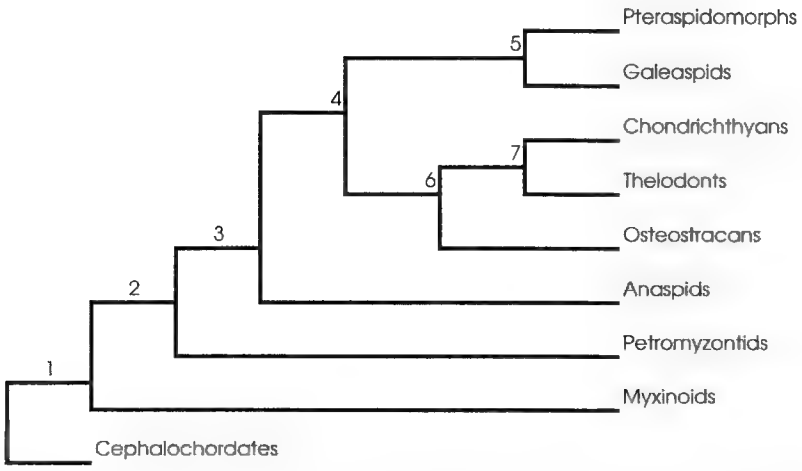

FIG. 8. — Hypothesis of phylogenetic relationships among craniates. 1, neural crest and its derivative; horny teeth. 2, nervous regulation of the heart; arcualia; oculomotor musculature; caudal fin with rays. 3, branchial chambers transversally elongated; (phosphatic) acellular bone. 4, mouth with inferior lip covered by articulated scales or tesserae; sensory-line system enclosed in canals. 5, ventral shield. 6, branchial openings covered with individual gill covers; heteroceral caudal fin; pectoral fin; cellular dermal bone with non-lamellar but cancellar base or with pulp cavity openings; bone covered with superficial dentinous tissue (mesodentine, metadentine or orthodentine). 7, micromeric dermal skeleton without differentiation between cranial and postcranial skeleton; two anterior nostrils (diplorhiny); anal fin.

Hypothèse de relations phylogénétiques entre les craniates. 1, crête neurale et ses dérivés, dents cornées. 2, régulation nerveuse du cœur, arcualia, musculature oculomotrice, nageoire caudale armée de rayons. 3, chambres branchiales allongées transversalement, os acellulaire (phosphaté). 4, lèvre inférieure de la bouche couverte d'écailles articulées ou de tessères, système de la ligne sensorielle enclos dans des canaux. 5, bouclier ventral. 6, ouvertures branchiales munies d'opercules individuels, nageoire caudale hétérocerque, nageoires pectorales, os dermique cellulaire à couche basale non-lamellaire mais cancellaire ou percée de foramens pour les cavités pulpaires, os couvert d'un tissu dentineux superficiel (mésodentine, métadentine ou orthodentine). 7, squelette dermique micromérique sans différenciation entre squelette crânien et postcrânien, deux narines antérieures (diplorhinie), nageoire anale.

The distribution of such characters as the presence of a nasopharyngeal or a nasohypophysial duct suggests that they are present in the pteraspidomorphs, since they occur in the petromyzontids and the osteostracans. The other solution is that it was lost more than once.

A relationship between anaspids and petromyzontids was suggested and it is still considered as a valid hypothesis (STENSIÖ, 1927; WÄNGSJÖ, 1952; JANVIER, 1981; JANVIER & BLIECK, 1979; FOREY, 1984). Characters, such as the branchial openings arranged in slanting row (character 29) or the presence of an annular cartilage (character 25) are here considered as primitive for the vertebrates. The present hypothesis rather suggests that anaspids are more derived because of their bony dermal skeleton and pectoral appendages.

One stable point of the analysis is the interrelationship of thelodonts and gnathostomes. They share a micromeric exoskeleton, without any anteroposterior differentiation (characters 10, 11). One may argue that micromery is a primitive state, but the PAUP analysis suggests the contrary. Micromery would be derived from a dermal skeleton with a cyclomorial growth pattern (mesomeric dermal skeleton).

The new thelodont morphology revealed by the Arctic forms (WILSON & CALDWELL, 1993) was not included in the present analysis. It is certain that these forms will have a great importance in our understanding of the agnathan evolution. From the present phylogenetic analysis, I predict that the pectoral appendages will lose of their significance as a character and that the olfactory apparatus and bone mesostructure will be more significant features.

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TABLE 1. Character matrix used in the PAUP 2.4.1 program analysis (SWOFFORD, 1985). The N values (irrelevant) are replaced in analysis by ? (unknown). All characters are unordered, and the option swap=global and multipars was set on. The result is illustrated in figures 7 and 8.

Matrice de caractères utilisée dans l'analyse à l'aide du logiciel PAUP 2.4.1 (SWOFFORD, 1985). Les valeurs N (non pertinent) sont remplacées par ? (inconnu). Tous les caractères sont non ordonnés et l'option "swap=global" et "multipars" a été appliquée. Le résulat est illustré par les figures 7 et 8.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Cephalochordates	0	0	0	0	N	0	N	N	0	N	0	N	0	N	0	0	0	0	1	0	0	0	0
Arandaspis	1	?	?	1	0	1	?	?	1	1	2	?	0	0	0	?	?	?	?	0	0	0	1
Astraspis	1	?	?	1	0	1	1	1	?	0	1	2	0	1	?	?	0	0	?	0	0	0	1
Eriptychius	1	?	?	?	?	1	1	1	?	0	1	2	0	1	?	?	?	?	?	?	?	?	?
Sacabambaspis	1	?	?	1	1	1	0	0	1	1	2	1	0	0	0	2	0	0	0	0	0	0	1
Cyathaspids	1	?	?	1	1	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0	0	0	1
Pteraspids	1	?	?	1	1	1	1	1	1	1	2	1	0	1	0	1	0	0	0	0	0	0	1
Anaspids	1	?	?	0	2	1	1	0	0	0	2	0	0	0	1	1	1	1	1	0	0	1	0
Galeaspids	1	?	?	2	?	1	1	0	1	1	?	0	1	?	?	?	?	?	?	?	?	0	?
Myxinoids	1	0	0	0	2	0	N	N	0	N	0	N	N	N	0	0	0	0	1	1	0	0	1
Osteostracans	1	1	?	2	2	1	0	1	0	0	2	2	1	0	1	2	2	0	1	0	1	2	0
Petromyzontids	1	1	1	1	2	0	N	N	0	N	0	N	N	N	1	2	0	0	1	1	1	0	1
Thelodonts	1	?	?	2	1	1	1	1	0	2	0	2	0	2	1	1	1	1	1	1	1	2	1
Chondrichthyans	1	1	1	2	2	1	0	1	0	2	0	2	0	2	1	2	2	1	1	1	1	1	1

	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Cephalochordates	0	N	0	N	N	N	N	N	N	N	N	N	0	N	N	N	0	0	0	0	N	N
Arandaspis	?	1	1	2	?	0	0	?	?	?	0	?	1	2	?	?	?	?	?	?	1	?
Astraspis	?	?	0	1	?	2	0	?	?	?	0	?	1	?	?	?	?	?	?	0	0	?
Eriptychius	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?
Sacabambaspis	0	1	1	2	1	0	0	1	1	?	0	?	1	2	0	1	1	1	1	0	1	?
Cyathaspids	0	1	0	1	1	2	1	1	?	0	0	?	2	2	0	2	0	0	?	0	0	?
Pteraspids	0	1	0	1	1	2	1	1	?	0	0	?	2	2	0	2	0	0	?	0	0	?
Anaspids	?	0	0	1	?	0	0	?	0	?	1	?	1	?	0	1	0	0	?	1	0	?
Galeaspids	?	?	0	0	1	1	0	1	0	0	1	0	2	0	?	?	0	0	?	?	0	1
Myxinoids	1	0	0	0	0	1	0	0	0	1	0	0	0	0	N	0	0	0	0	0	0	0
Osteostracans	?	1	1	1	1	0	0	0	0	1	1	1	2	2	N	0	1	1	1	0	0	1
Petromyzontids	1	0	0	0	0	0	0	0	0	1	1	1	1	1	N	0	0	0	1	1	0	0
Thelodonts	?	?	1	1	1	1	0	1	?	0	0	?	2	1	2	2	0	0	?	?	0	?
Chondrichthyans	0	N	N	0	N	N	0	1	1	0	0	1	2	N	2	2	0	0	1	0	0	1

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The distribution of the vertebrates in the Late Ordovician and Early Silurian palaeobasins of the Siberian Platform

by Valentina KARATAJUTE-TALIMAA and Nikolaj PREDTECHENSKYJ

(A contribution to IGCP 328-Palaeozoic Microvertebrates)

Abstract. — Scattered vertebrate exoskeletal elements occur in the facies of bar belt, restricted shallow shelf, lagoon belt, coastal belt and underwater part of alluvial plains of the Ordovician and Silurian of the Siberian Platform. During Late Ordovician times and in the beginning of the Early Llandovery, the Astraspidida played a significant role in vertebrate faunas. On the small territory of the Niuya-Beresovo area, thelodonts and the oldest known Gnathostomata -acanthodians and chondrichthyans– were found in Lower Llandoverian rocks. Rich vertebrate assemblages distributed on large areas of the southern part of the Siberian Platform are characteristic for Middle Llandovery beds. A considerable turn in vertebrate assemblages took place during the Late Llandovery, when mongolepidids (Chondrichthyans) and several new genera of acanthodians appeared. The generic composition of Wenlockian vertebrate assemblages is still unclear. The occurrence of new thelodonts is established. The aniseed-oil method of identification for vertebrate microremains is described. It is concluded that in the first half of the Early Palaeozoic, the major morphogenetic types of the dermal skeleton, the main modes of growth and also various types of tissues were already present.

Keywords. — Vertebrata, Agnatha, Chondrichthyes, Acanthodii, Ordovician, Silurian, Siberia, palaeoecology, biostratigraphy.

La répartition des Vertébrés dans l'Ordovicien terminal et le Silurien inférieur des paléobassins de la Plateforme Sibérienne

Résumé. — Des restes d'éléments exosquelettiques isolés se rencontrent dans les faciès de lagons, de barrière côtière, et de plaine alluviale sous-marine de l'Ordovicien et du Silurien de Sibérie. Pendant l'Ordovicien supérieur, et au début du Llandovery inférieur, les Astraspida occupèrent une place importante dans les faunes de vertébrés. Sur le territoire restreint de la région de Niuya-Beresovo, des thélodontes et les plus anciens Gnathotomata connus (Acanthodiens et Chondrichthyens) ont été trouvés dans le Llandovery inférieur. De riches assemblages de Vertébrés, distribués sur de vastes régions de la partie Sud de la Plateforme Sibérienne, sont caractéristiques des niveaux du Llandovery moyen. Un changement considérable dans la composition des faunes de Vertébrés s'est produit au Llandovery supérieur, quand les mongolépidides (Chondrichthyens) et plusieurs nouveaux genres d'acanthodiens apparurent. La composition générique des faunes de Vertébrés wenlockiennes n'est toujours pas claire, mais l'apparition de nouveaux Thélodontes est établie. La méthode d'identification des microrestes de Vertébrés par immersion dans l'essence d'anis est exposée. Enfin, il est conlu que dans la première moitié du Paléozoïque inférieur, les principaux types morphogénétiques de squelette dermique, les principaux modes de croissance, ainsi que divers types de tissus durs étaient déja présents.

Mots-clés. — Vertébrés, Agnatha, Chondrichthyes, Acanthodii, Ordovicien, Silurien, Sibérie, paléoécologie, biostratigraphie.

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INTRODUCTION

The Siberian Platform is one of the largest areas where Silurian deposits are exposed. These deposits cover more than two million square kilometres and form an enormous Middle Siberian sedimentary basin. In 1972 the research program on Silurian deposits started on this territory, in the framework of the project "Ecostratigraphy". This program was headed by N. PREDTECHENSKYJ (St. Petersburg) and Y. TESSAKOV (Novosibirsk). Early results have been published, but the publications do not contain data on the vertebrates. The field-work during which the vertebrates were collected started in 1982 and was carried on in 1984 and 1986. The rock samples containing vertebrates were collected in outcrops and later processed with acid. They come from the following sections: Tchuna-Biriussa (6), Angara-Ilim (7), Niuya-Beresovo (8) and Maimetcha (12) (Fig. 1). The material from the Turukhansk (4), Tunguska (5), Viliuj (9) and Moyero (11) areas was sampled when looking for other taxa and therefore does not yield extensive data.

VERTEBRATE OCCURRENCES

Discrete elements of vertebrate exoskeleton in the Late Ordovician and Early Silurian are bound to the following facies in the paleobasin: the bar belt, restricted shallow shelf, lagoon belt (saline and brackish lagoons), coastal belt and underwater part of alluvial plains (Fig. 2). The sedimentological pattern of the Silurian basin of the Siberian Platform has been published by PREDTECHENSKYJ (1989).

In the upper parts of the Ordovician, tesserae of astraspidids (Astraspididae n. g., n. sp. 1) were found, along with conodonts, pelecypods, gastropods and brachiopods, in borehole cores from drillings through the marine shallow water deposits in a small area of the Viliuj region (9, Fig. 1). In the same area, at the base of the Silurian, occur conglomerates in which tesserae of Astraspididae n. g., n. sp. 2 were found together with Silurian conodonts. The Astraspididae n. g. (*Tesakoviaspis concentrica* Karatajute-Talimaa *nomen nudum*, KARATAJUTE-TALIMAA, 1978, Pl. 32, Figs 4-7) is characteristic of the basal part of the Silurian section to the West, in the Tunguska area (5), on the Lower Tchunku (Nizhniaya Tchunku) River. The same species has been discovered in a sandstone layer of the bed 42 of the Old Balturino outcrop in the Tchuna-Biriussa area (6), together with a shelly fauna (Fig. 3).

It can be concluded that in the Late Ordovician and at the beginning of the Early Llandovery astraspidids are prevailing (Figs. 4, 5) among vertebrates. Some acanthodian scales found in the supposedly Ordovician part of the Balturino Formation (Fig. 3) could eventually occur in the samples.

A section on the river Niuya (8) in South Yakutya (Fig. 6) is of particular interest. In the Melitchan Formation (Lower Llandovery) were found the oldest known gnathostome scales. They belong to a new chondrichthyan genus and a new acanthodian genus, and occur with thelodont scales. These minute vertebrate remains come from the open shallow shelf facies, and the outer and inner zones of the shoal. The rocks which yield these remains are metasomatic dolomites and dolomitized limestones containing relics of a primary nodular texture, diagenetic flint concretions together with conodonts, cephalopods, solitary tetracorals, brachiopods and traces of

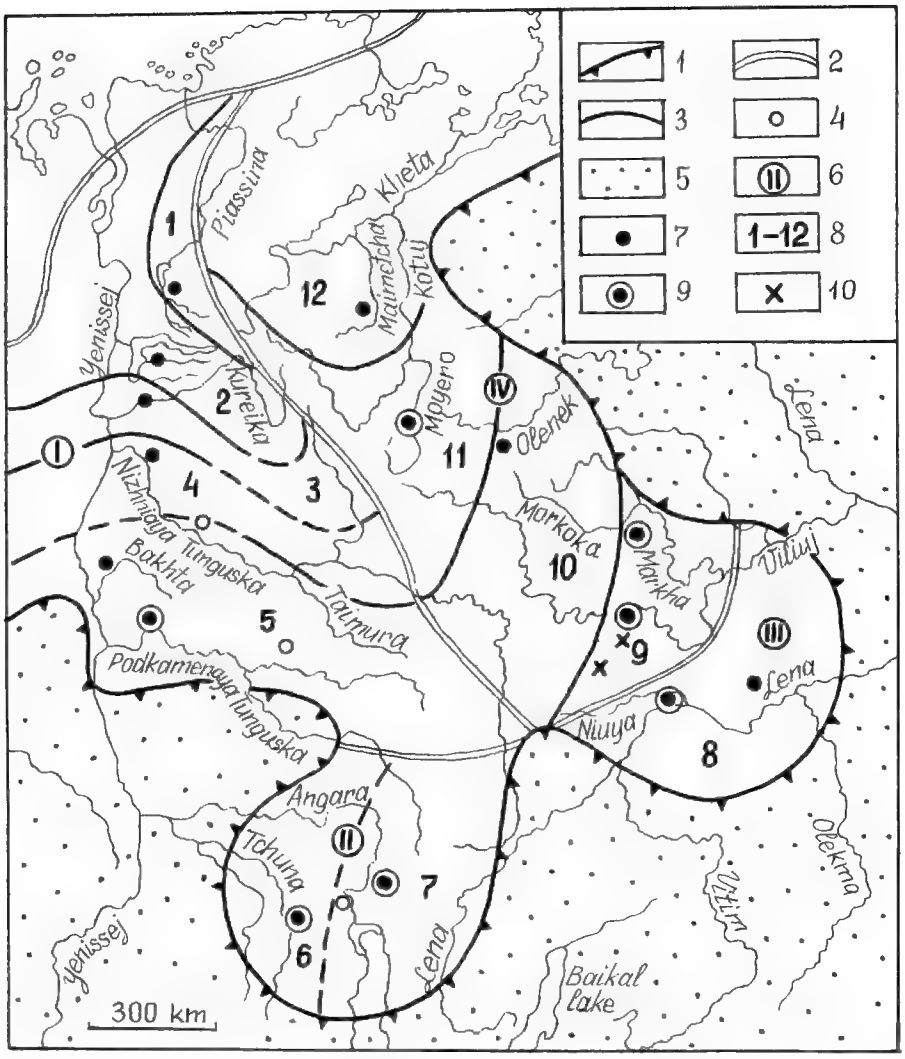
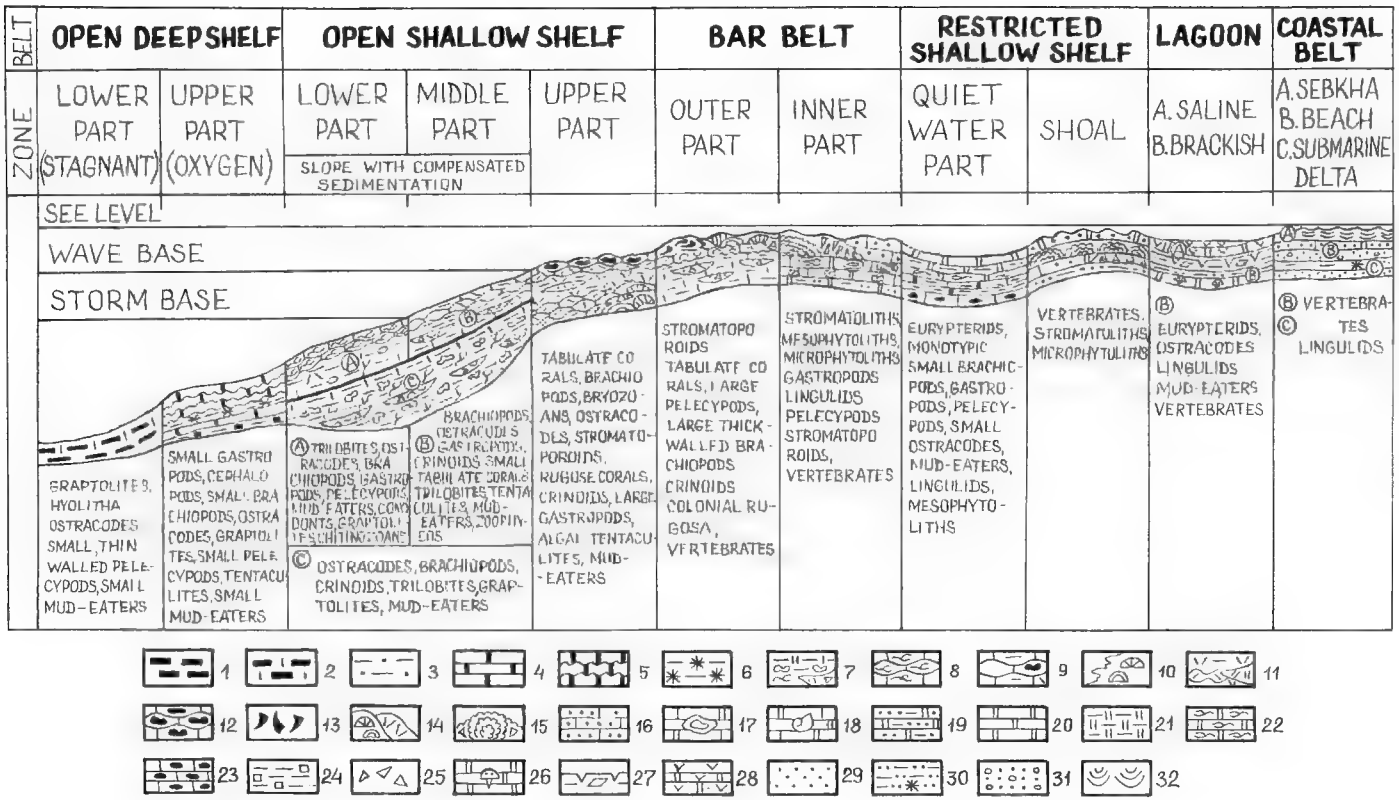


FIG. 1. — Stratigraphical subdivision of the Siberian Platform for the Silurian system, and geographical position of the sections. 1, boundary of the basins (stratigraphic regions); 2, boundaries of the sub-regions; 3, boundaries of the areas; 4, Lower Silurian vertebrate localities; 5, upland areas; 6, sub-regions; 7, reference sections; 8, areas (1 – Norilsk, 2 – Igarka, 3 – Kureika, 4 – Turukhansk, 5 – Tunguska, 6 – Tchuna-Biriussa, 7 – Angara-Ilim, 8 – Niuya-Beresovo, 9 – Viliuj, 10 – Morkoka, 11 – Moyero, 12 – Maimetcha); 9, reference sections with Lower Silurian vertebrates; 10, Upper Ordovician vertebrate localities.

Subdivisions stratigraphiques du Silurien de la Plateforme Sibérienne et position géographique des sections. 1, limite des bassins (régions stratigraphiques); 2, limites des sous-régions; 3, limite des zones; 4, localités d'âge silurien inférieur; 5, zones émergées; 6, sous-régions; 7, sections de référence; 8, zones (1 – Norilsk, 2 – Igarka, 3 – Kureika, 4 –Turukhansk, 5 – Tunguska, 6 – Tchuna-Biriussa, 7 – Angara-Ilim, 8 – Niuya-Beresovo, 9 – Viliuj, 10 – Morkoka, 11 –Moyero, 12 – Maimetcha); 9, sections de référence pour les Vertébrés du Silurien inférieur; 10, gisements à Vertébrés de l'Ordovicien inférieur.


BELT
OPEN DEEPSHELF
OPEN SHALLOW SHELF
BAR BELT
RESTRICTED SHALLOW SHELF
LAGOON
COASTAL BELT
ZONE
LOWER PART (STAGNANT)
UPPER PART (OXYGEN)
LOWER PART
MIDDLE PART
UPPER PART
SLOPE WITH COMPENSATED SEDIMENTATION
OUTER PART
INNER PART
QUIET WATER PART
SHOAL
A. SALINE
B. BRACKISH
A. SEBKHA
B. BEACH
C. SUBMARINE DELTA
SEE LEVEL
WAVE BASE
STORM BASE
GRAPTOLITES, HYOLITHA OSTRACODES SMALL, THIN WALLED PELECYPODS, SMALL MUD-EATERS
SMALL GASTROPODS, CEPHALOPODS, SMALL BRACHIOPODS, OSTRACODES, GRAPTOLITES, SMALL PELECYPODS, TENTACULITES, SMALL MUD-EATERS
Ⓐ TRILOBITES, OSTRACODES, BRACHIOPODS, GASTROPODS, PELECYPODS, MUD-EATERS, CONODONTS, GRAPTOLITES, CHITINOZOANS
Ⓑ BRACHIOPODS, OSTRACODES, GASTROPODS, CRINOIDS, SMALL TABULATE CORALS, TRILOBITES, TENTACULITES, MUD-EATERS, CONODONTS
Ⓒ OSTRACODES, BRACHIOPODS, CRINOIDS, TRILOBITES, GRAPTOLITES, MUD-EATERS
TABULATE CORALS, BRACHIOPODS, BRYOZOANS, OSTRACODES, STROMATOPOROIDS, RUGOSE CORALS, CRINOIDS, LARGE GASTROPODS, ALGAL TENTACULITES, MUD-EATERS
STROMATOPOROIDS TABULATE CORALS, LARGE PELECYPODS, LARGE THICK-WALLED BRACHIOPODS CRINOIDS COLONIAL RUGOSA, VERTEBRATES
STROMATOLITHS MESOPHYTOLITHS, MICROPHYTOLITHS GASTROPODS LINGULIDS PELECYPODS STROMATOPOROIDS, VERTEBRATES
EURYPTERIDS, MONOTYPIC SMALL BRACHIOPODS, GASTROPODS, PELECYPODS, SMALL OSTRACODES, MUD-EATERS, LINGULIDS, MESOPHYTOLITHS
VERTEBRATES, STROMATOLITHS, MICROPHYTOLITHS
Ⓑ EURYPTERIDS, OSTRACODES LINGULIDS MUD-EATERS VERTEBRATES
Ⓑ VERTEBRATES
Ⓒ LINGULIDS
1 2 3 4 5 6 7 8 9 10 11
12 13 14 15 16 17 18 19 20 21 22
23 24 25 26 27 28 29 30 31 32

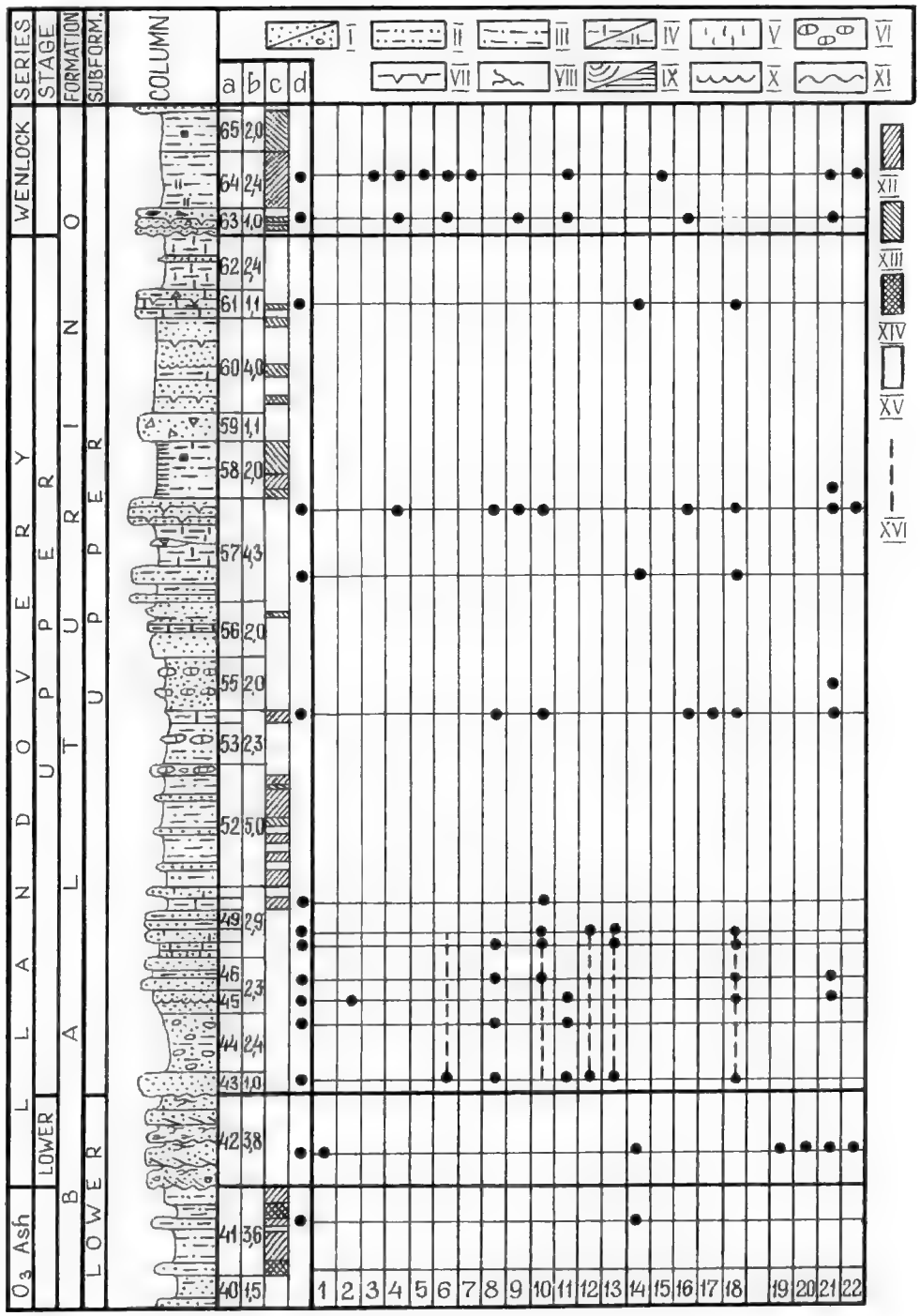
"mud-eaters". Bionomic peculiarities of the basal member of Melitchan Formation show that it has been formed in the upper, wavy zone of the open shelf and in a near-shore shallow water environment.

In the outcrop near Old Balturino village (bed 42), in the Tchuna-Biriussa area (6), vertebrates of Lower Llandovery age were found in the cross-bedded, poorly sorted quartzitic sandstones, rhytmically intercalated with siltstones and silty sandstones, rich in traces of "mud-eaters". They were deposited on the margins of the basin, most probably in an underwater delta environment.

The Middle Llandovery beds are characterized by comparatively rich vertebrate assemblage with *Loganellia? moskalenkoae* Karatajute-Talimaa, *L. sibirica* Karatajute-Talimaa, *Elegestolepis conica* Karatajute-Talimaa and Acanthodii n. g. A (Figs. 4, 5, 6). Tesserae with areal growth, probably belonging to the Astraspidida, are also present (Fig. 7E, F). This assemblage comes from the near-shore and lagoonal facies and is distributed over a significantly large territory (Fig. 4).

FIG. 2. — Facies model of the Silurian paleobasin of the Siberian Platform (after PREDTECHENSKYJ, 1989). 1, argillites: black, carbonaceous (up to 12%), containing pyrite, horizontally laminated; 2, argillites; dark-grey, weakly carbonaceous (2-5%), with interlayers of grey marls, sometimes containing calcareous concretions and dispersed pyrite, horizontally and wavy bedded; 3, argillites; greenish-grey, calcareous, laminated, sometimes containing pyrite; 4, grey, argillaceous, pelitomorphic limestones, containing pyrite; 5, muddy, pelitomorphic limestones, hillocky bedded with diastems; 6, argillites; purple to red, horizontally bedded; 7, marls containing concretions and lenticular interlayers of muddy limestones, abundant traces of "mud-eaters", lenses of biomorphic authigenous brecciae; 8, argillaceous limestones, nodular, with traces of "mud-eaters"; 9, argillaceous limestones; nodular, detritous, with lenticular interlayers of marls, traces of "mud-eaters", sometimes containing siliceous concretions; 10, bioherms; coral stromatoporid, algal, dilophoidal; 11, nodular limestones and detritic marls with lenses of massive detritic limestones; 12, nodular limestones; detritous, containing flintstone concretions; 13, large massive brachiopod and/or pelecypod-bearing banks; 14, stromatoporid coral and algal biostroms with traces of their destruction; 15, bedded and bun-shaped stromatolites with authigenous calcareous-dolomitic breccias; 16, oolitic limestones, 17, limestones; black odorous oncolitic, often dolomitized, 18, dolomitic limestones; black with gastropods; 19, argillaceous-silty dolomites and dolomitic marls; 20, dolomites; massive, fetid; 21, dolomitic marls (domerites); 22, argillaceous dolomites with traces of "mud-eaters"; 23, microphytolitic limestones, 24, argillites; dark grey horizontally bedded, containing pyrite, 25, calcareous-dolomitic, authigenous brecciae, 26, *Eurypterus*-dolomites and domerites; 27, argillites and siltstones with shrinkage cracks and caverns due to dissolution of halite; 28, gypsum-bearing dolomites and gypsum; 29, sandstones; massive, cross-bedded; 30, variegated siltstones; 31, 32, sandstones; massive, cross-bedded, containing pebbles, with intercalations of thin-laminated argillaceous dolomites, domerites and gypsum with wide shrinkage cracks.

Modèle de faciès du paléobassin Silurien de la Plateforme Sibérienne (d'après PREDTECHENSKYJ, *1989). 1 argilites : noir, avec des traces de charbon (jusqu'à 12%), pyriteuses, laminées horizontalement 2, argilites : gris-sombre faiblement charbonneuses (2-5%) interstratifiées avec des marnes grises, contenant parfois des concrétions calcaires et des traces de pyrite, en strates horizontales et ondulées, 3, argilites : gris verdâtre, carbonatées, laminées, contenant parfois de la pyrite ; 4, calcaires gris, argileux, pélitomorphes, pyriteux 5, calcaires argileux, pelitomorphes, lités en hillocks avec des diastèmes ; 6, argilites ; rouges à violettes, litées horizontalement ; 7, marnes contenant des concrétions et des lentilles de calcaires argileux, avec de nombreuses traces d'organismes limivores et des lentilles de brèches authigéniques biomorphes ; 8, calcaires argileux, avec traces d'organismes limivores, 9, calcaires argileux : noduleux, détritiques, avec des lentilles de marne, contenant des traces d'organismes limivores et parfois des concrétions siliceuses ; 10, bioherms : à coraux, stromatoporides et algues, dilophoïdes ; 11, calcaires noduleux et marnes détritiques avec lentilles de calcaire détritique massif, 12, calcaires noduleux : détritiques, à concrétions de silex ; 13, grands bancs massifs riches en Brachiopodes et/ou Bivalves ; 14, bioherms à coraux stromatoporides et biostromes algaires avec des traces de leur destruction ; 15, stromatolites lités et en forme de beignet avec des brèches authigènes calcaires à dolomitiques ; 16, calcaire oolithique, 17, calcaires : noirs, fétides, oncholithiques, souvent dolomitiques ; 18, calcaires dolomitiques, noir, avec des gasteropodes ; 19, dolomies argileuses à silteuses et marnes dolomitiques ; 20, dolomies : massives, fétides ; 21, marnes dolomitiques (domérites) ; 22, dolomies argileuses avec traces d'organismes limivores ; 23, calcaires microphytolitiques ; 24, argilites : gris-sombre, litées horizontalement, pyriteuses ; 25, brèches authigènes calcaires dolomitiques ; 26, dolomies à* Eurypterus *et domérites ; 27, argilites et silts à fentes de dessication et lacunes dues à la dissolution de cristaux de sel gemme ; 28, dolomies gypseuses et gypse ; 29, grès : massifs, à stratifications entrecroisées ; 30, silts bariolés ; 31, 32, grès : massifs, à stratifications entrecroisées, contenant des galets, avec des intercalations de dolomies finement litées, de domérites et de gypse, et avec des fentes de dessication.*


SERIES
STAGE
FORMATION
SUBFORM.
COLUMN
a
b
c
d
I
II
III
IV
V
VI
VII
VIII
IX
X
XI
XII
XIII
XIV
XV
XVI
WENLOCK
LLANDOVERY
O3 Ash
UPPER
LOWER
BALTURINO
UPPER
LOWER
65 2,0
64 2,4
63 1,0
62 2,4
61 1,1
60 4,0
59 1,1
58 2,0
57 4,3
56 2,0
55 2,0
53 2,3
52 5,0
49 2,9
46
45 2,3
44 2,4
43 1,0
42 3,8
41 3,6
40 1,5
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22

In the Niuya River outcrops, the most abundant vertebrate remains of Middle Llandovery age are met with at the base of the Utakan Formation (see Fig. 6, outcrop 156, beds 37, 38; outcrop 157, beds 26-42). Here they occur in clayey, silty, dolomitic limestones containing rare, small tabulate corals, brachiopods, gastropods and ostracods. Obviously the deposits were formed in a shallow water environment with an abnormal salinity. This vertebrate assemblage, together with ostracodes and traces of "mud-eaters" is less frequent in limestone layers, among the variegated siltstones and dolomitic argillites which were evidently formed in lagoonal conditions.

The richest vertebrate samples of this level were collected in the vicinity of the Tushama station (7, Figs. 1, 4). They come from variegated (green with reddish, brown spots) and red siltstones containing quartz grains, as well as from poorly sorted, grey quartzitic quartz sandstones with a calcareous cement. Numerous lingulids and pelecypods were found along with the vertebrate remains. These beds were probably formed in lagoons with a low salinity, in an underwater delta region.

In the Late Llandovery beds occur remains of numerous and various acanthodians (at least two new genera and 4-5 new species), mongolepidid chondrichthyans (two new genera), a new species of thelodonts (*Loganellia* ex gr. *scotica* n. sp. 1), minute scales of *Elegestolepis conica* Karatajute-Talimaa and numerous tesserae of a new genus, possiby belonging to a lower chordate? (Figs. 4, 5). The most complete assemblage occurs in the Tchuna-Biriussa (6) area. In the Old Balturino outcrop (Fig. 3) occur some layers intercalated with "bone-beds". Vertebrates come from brackish lagoonal deposits and underwater delta sediments. Horizontally laminated, variegated and greyish green siltstones and marls, and horizontally bedded sandstones with calcareous concretions are considered as brackish lagoonal deposits. Unsorted, cross-bedded, or massive and indistinctly horizontally bedded, quartz-bearing quartzitic sandstones with "bone-bed" interlayers represent underwater delta deposits.

In other areas of the paleobasin poorer vertebrate assemblages were found in the near-shore marine deposits of the Upper Llandovery (Fig. 4).

FIG. 3. — Distribution of the vertebrates in the Old Balturino outcrop (upper part). I, quartz sandstone: fine and medium-grained (a), with quartz and quartzitic pebbles (b); II, sandy siltstone; III, siltstone; IV, marl: calcareous (a), dolomitic (b); V, calcareous cement; VI, limestone interlayer and separate calcareous concretions; VII, undulating ripples marks; VIII, traces of "mud-eaters"; IX, cross-bedding (a), horizontal bedding (b); X, mud-cracks; XI, erosion surface. Colour of the rocks. XII, green; XIII, red; XIV, variegated, spotted, XV, neutral; XVI, from talus. Taxa: 1, *Tesakoviaspis concentrica* Karatajute-Talimaa; 2, *Loganellia* ex gr. *scotica* (n. sp. 1); 3, *Loganellia* cf. *asiatica* (Karatajute-Talimaa); 4, *Helenolepis?* n. sp.; 5, *Helenolepis?* sp.; 6, *Elegestolepis conica* Karatajute-Talimaa; 7, *Elegestolepis?* sp., 8, Mongolepididae n. g. A; 9, Mongolepididae n. g. B; 10, Acanthodii n. g. B, sp. 1, 11, Acanthodii n. g. B, 12, Acanthodii n. g. C, 13, Acanthodii indet. (tesserae), 14, Acanthodii indet.; 15, acanthodii n. g.?; 16, Astraspidida? indet.; 17, cf. Osteostraci indet.; 18, lower Chordata? n. g.; 19, gastropods; 20, conodonts; 21, nautiloids; 22, lingulids. a, bed; b, thickness; c, colour of the rocks; d, position of the sampling.

Répartition des Vertébrés dans le gisement du Vieux Balturino (partie supérieure). I, grès quartzeux: grain fin à moyen (a), avec galets de quartz ou de quartzite (b); I, silt sableux; III, silt; IV, marne: calcaire (a), dolomitique (b); V, ciment calcaire, VI, interstrates calcaires et concrétions calcaires séparées; VII, ripple-marks ondulées; VIII, traces d'organismes limivores, IX, stratifications entrecroisées (a), couches horizontales (b); X, fentes de dessication; XI, surface d'érosion. Couleur des roches: XII, verte; XIII, rouge; XIV, bariolées, tachetées; XV, neutre; XVI, du talus. Taxons: 1, Tesakoviaspis concentrica *Karatajute Talimaa; 2,* Loganellia ex gr. scotica *(n. sp. 1); 3,* Loganellia *cf.* asiatica *(Karatajute-Talimaa); 4,* Helenolepis *? n. sp.; 5,* Helenolepis *? sp; 6,* Elegestolepis conica *Karatajute-Talimaa; 7,* Elegestolepis *? sp.; 8, Mongolepididae n. g. A; 9, Mongolepididae n. g. B; 10, Acanthodii n. g. B, sp. 1; 11, Acanthodii n. g. B; 12, Acanthodii n. g. C; 13, Acanthodii indet (tessères), 14, Acanthodii indet.; 15, Acanthodii n. g. ?; 16, Astraspidida ? indet.; 17, cf. Osteostraci indet.; 18, Chordata inférieurs ? n.g.; 19, Gastéropodes; 20, Conodontes; 21, Nautiloides; 22, Lingulides. a, couche; b, épaisseur; c, couleur de la roche; d, position de l'échantillonnage.*

	area	4 Turukhansk	5 Tunguska	6 Tchuna-Biriussa	7 Angara-Jlim	8 Niuya-Beresovo	9 Viliuj	11 Moyero
WENLOCK	KHAKOM	Acanthodii g.n. B ?	Loganellia ex gr. scotica (sp.n.2), Acanth. g.n.B.	Upper Balturino subformation: Loganellia cf. asiatica, Helenolepis sp.n., Elegestolepis ?, Mongolepididae g.n., Acanth.g.n.B		Niuya formation: Acanthodii ind.		
LLANDOVERY	AGIDYJ	Loganellia, Elegestolepis, Acanth. g.n. B.		Upper Balturino subformation: Loganellia ex gr. scotica (sp.n.1), Elegestolepis conica, Mongolepididae g.n. Acanth.g.n.B,C, Chordata g.n.	Rassokha formation: Loganellia ex gr. scotica (sp.n.1), Acanthodii g.n. B, Chordata g.n.	Utakan formation: Acanthodii g.n. B?		Loganellia ex gr. scotica, L. sibirica
	KHAASTYR		Loganellia? moskalenkoae, L. sibirica, Astraspidida? Acanth.g.n.A.	Upper Balturino subformation: ↓ ?	Rassokha formation: Loganellia? moskalenkoae, L. sibirica, Elegestolepis conica, Acanth.g.n.A	Utakan formation: Loganellia? moskalenkoae, L. sibirica, Astraspidida ?, Elegestolepis conica, Elasmobranchii g.n. Acanth.g.n.A		
	MOYEROKAN		Tesakoviaspis concentrica	Upper Balturino subformation: Tesakoviaspis concentrica	Rassokha formation	Melitchan f.: Loganellia sibirica, Astraspidida ?, Elasmobr. g.n., Acanthodii g.n.A.	Astraspididae g.n., sp.n. 2	
							Astraspididae g.n., sp.n.1	

FIG. 4. — Vertebrate assemblages in the Lower Silurian of the Siberian Platform.

Assemblages de Vertébrés dans le Silurien inférieur de la Plateforme Sibérienne.

O_3 Ash	LLANDOVERY L.	LLANDOVERY M.	LLANDOVERY U.	WENLOCK	Species / Genus / Family / Order / Sub-class	class subclass
	MOYERO-KAN	KHASTYR	AGIDYI	KHAKOM		
—					Astraspididae g.n., sp.n. 1	HETEROSTRACI
	—				Astraspididae g.n., sp.n. 2	
	—-				Tesakoviaspis concentrica	
	—	—			Astraspidida ? indet.	
	—	—			Elasmobranchii g.n.	CHONDRICHTHYES
		—	—		Elegestolepis conica	
			—	—	Elegestolepis ? sp.	
			—		Mongolepididae g.n. A.	
				—	Mongolepididae g.n. B.	
	—	—	--		Loganellia sibirica	THELODONTI
		--	—		Loganellia ex gr. scotica	
			—		Loganellia ex gr. scotica 1	
				—	Loganellia ex gr. scotica 2	
		—			Loganellia ? moskalenkoae	
				—	Loganellia cf. asiatica	
				—	Helenolepis ? sp.n.1	
	—	—			Acanthodii g. n. A.	ACANTHODII
			—		Acanthodii g.n. B ,sp. 1	
		--	—	—	Acanthodii g.n. B	
			—	—	Acanthodii g.n. B ?	
			—		Acanthodii g.n. C	
—	—			—	Acanthodii ind.	
			—		Lower Chordata ? g.n.	
—	—				phosphatic nodules	

FIG. 5. — Distribution of the vertebrates in the Upper Ordovician and Lower Silurian of the Siberian Platform.
Répartition des Vertébrés dans l'Ordovicien supérieur et le Silurien inférieur de la Plateforme Sibérienne.

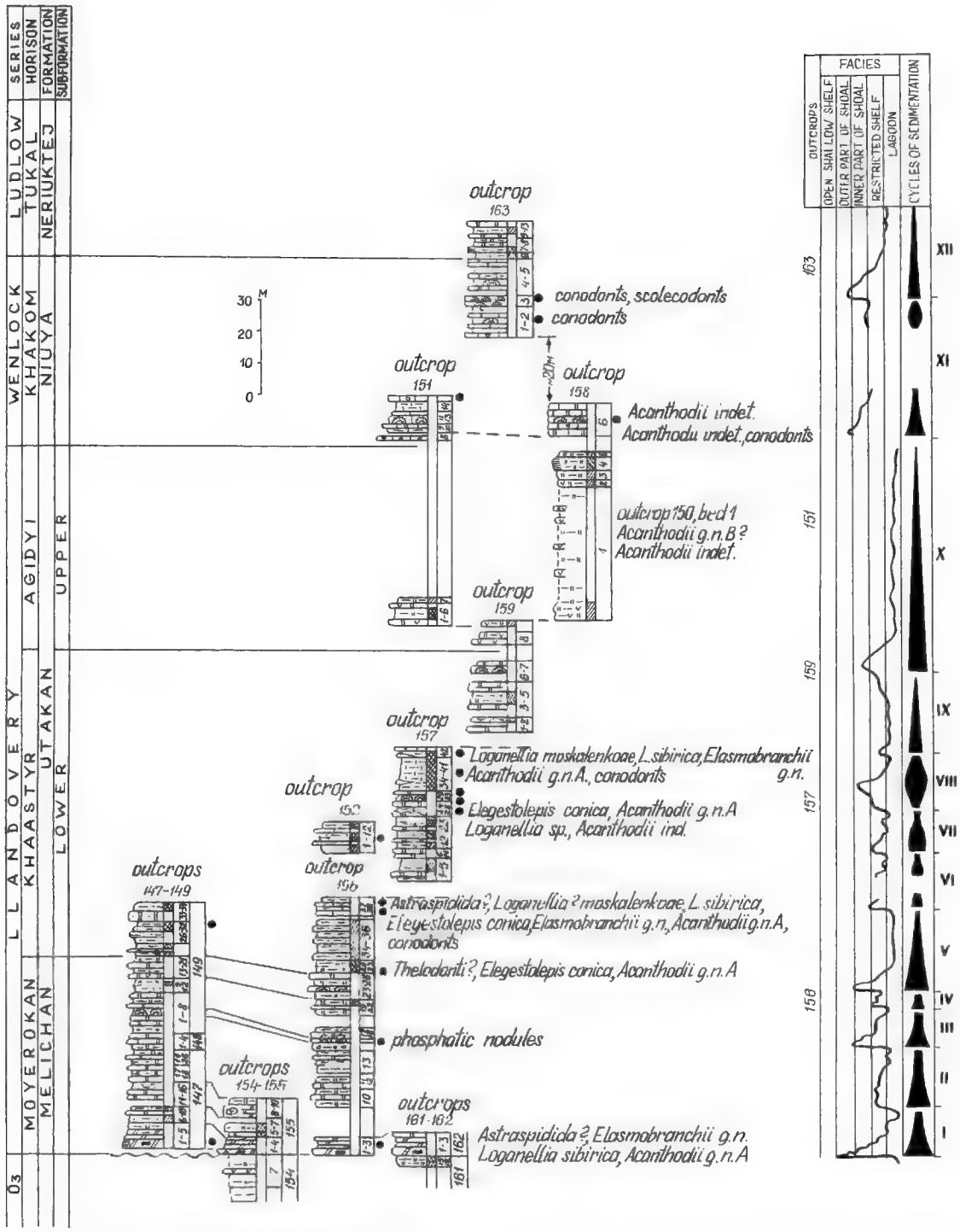


FIG. 6. — Distribution of the vertebrates in the outcrops of the Niuya and Lena rivers (outcrop 163). For explanation of lithological composition of the rocks in the sections, see Figures 2 and 3.

Répartition des Vertébrés dans les gisements des rivières Niuya et Lena (gisement 163). Pour les explications concernant la composition lithologique des sections, voir figures 2 et 3.

The generic and specific content of the vertebrates in Wenlock beds is not yet fully studied. According to the data from three areas, 4, 5 and 6 (Fig. 4), the Wenlock assemblage includes new species of thelodonts – *Loganellia* ex gr. *scotica* n. sp. 2, *L.* cf. *Asiatica* Karatajute-Talimaa and *Helenolepis?* n. sp. 1, and the same acanthodian and chondrichthyan genera (6) as in the Late Llandovery beds. The Wenlock vertebrate assemblage is most complete in the Old Balturino outcrop (Fig. 3).

Outside the Siberian Platform similar vertebrate assemblages have been discovered at the top of the Ordovician and in the Llandovery of Tuva, as well as in the Upper Llandovery of northwestern Mongolia.

Astrapidid tesserae occur in the Upper Ordovician of Tuva. In the Llandovery of this region, there are frequently thelodonts, acanthodians and chondrichthyans (mongolepidids included), which resemble those from the Siberian Platform. In the Upper Llandovery assemblage of Mongolia, the mongolepidid chondrichthyans (three genera) are abundant, and acanthodians are represented by the same Acanthodii n. g. B.

METHODS OF STUDY

The studied collection of early vertebrate remains consists exclusively of micro- and mesomeric tesserae and scales obtained by rock dissolution. As there is a very large number of discrete exoskeletal elements which vary in shape and structure, a specific method should be applied to define their systematic position. Recently the interest in vertebrates micro-remains has largely increased, and it would be reasonable to consider in detail the methods for their identification. The monographic description of the material is, however, planned to be prepared for publication in 1998.

At first, the remains should be visually identified according to their morphological features. Such a rough sorting of the material allows to establish the vertebrate group contents in respective samples. Later, such work should be made on samples of one and the same geological unit of uniform or almost uniform lithological composition, *i.e.* of a bed, a number of beds, or a member of a formation. It is recommended to study very large samples to avoid including into the hypodigm of a species elements belonging to another closely related species. It is necessary to establish the limits of the morphological variability in sets of tesserae and scales, *i.e.* to get and idea of the set of exoskeletal elements forming the squamation. In the exoskeleton of various early vertebrates which consist of micro- and mesomeric ossifications, the degree of variability of the elements may be different.

Then should follow the study of the inner structure of the remains and the definition of the mode of growth of the micro- and mesomeric exoskeleton elements. Investigating the inner structure of the dermal elements of a vertebrate is quite necessary for the identification of its systematic position, as the external aspect does not always permit to assign the remains to a particular group. Usually, sections should be made, *i.e.* some vertical and horizontal sections of tesserae or scales coming from different parts of the animal. If the skeletal element is light in colour and comparatively thin, it may be placed into aniseed oil, and studied under the microscope. Illuminated from behind it is partly transparent and many details of the inner structure

become visible. In this way, it is possible, without sectioning, to get an idea on the presence of canals, thinner tubuli and cavities, and to identify the presence and length of pulp cavities, osteocyte lacunae and type of dentine. The remains which are black in colour, recrystallized or with heavy iron content, as well as thicker scales and tesserae with superpositional growth cannot be studied in this way. Therefore, thin sections should be made.

Most microremains from the Llandovery and Wenlock rocks of the southern part of the Siberian Platform (Old Balturino and Tushama outcrops and those along the river Niuya) are suitable for histologic studies. Since the remains are white, yellowish and brownish in colour, numerous sections were made, whereas very fine scales and tesserae (0.2-1.2 mm in diametre) of astraspidids, thelodonts and chondrichthyans with comparatively thin base were studied under a microscope in aniseed oil. In the latter case one can observe a cavity or a canal at different levels and along its entire length, by changing the focus, which is not possible in sections. It is also important that such studies can be repeated. However, it must be pointed out that a skeletal element should not be kept in aniseed oil for a long time. After sketching or photographying, it should be carefully washed in alcohol. In order to have a full picture of the microstructure, a series of photographs made at different focus levels is needed. The sketch can be done in such a way that the cavity or canal can be shown in its total extent. The method is illustrated by sketches in figures 7 and 8, *i.e.* sketches of tesserae and scales immersed in aniseed oil during drawing.

GROWTH AND STRUCTURE OF THE SKELETAL ELEMENTS

The available material of Astraspididae allowed us to establish the growth pattern of tesserae during ontogeny, starting from a single primordial tubercle, almost undistinguishable from thelodont scales, and ending with completely formed, complex tesserae. Tesserae of different species of a new genus of Astraspididae (n. sp. 1, n. sp. 2 and *Tesakoviaspis concentrica*) differ from one another in shape and size, as well as in the number and density of the tubercles.

Figure 7A shows a tessera of Astraspididae g. n., sp. n. 1 in an early stage of development, revealing a big primordial tubercle with dentine tubules which resemble those of orthodentine.

FIG 7. — Tesserae of Astraspidida. A, Astraspididae n. g., n. sp. 1, Nr10-098, Middle Morkoka area (9 in Figure 1), bore-hole 151, depth 63.7 m., Upper Ordovician, Bura horizon; B, *Tesakoviaspis concentrica* Karatajute-Talimaa, Nr 10-099, Tchuna-Biriussa area (6 in Figure 1), outcrop Old Balturino, bed 42, Lower Silurian, Lower Llandovery, Lower Balturino Subformation; C, D, Astraspididae n. g., n. sp. 2, Nr10-100 and 10-101, area between Markha and Morkoka rivers (9 in Figure 1), bore-hole 412, depth 315 m., Lower Silurian, Lower Llandovery; E, F, Astraspidida? n. g., Nr 10-102 and 10-103, Niuya-Beresovo area (8 in Figure 1), Niuya River, outcrop 157, bed 37, Lower Silurian, Middle Llandovery, Lower Utakan Subformation. All illustrations of tesserae based on specimens immersed in aniseed oil.
Abbr.: pt, primordial tubercle; t, tubercles of areal zones of growth; dt, tubules in orthodentine; pc, pulp cavities filled by osteodentine (?).

Tessères d'Astraspidida A, Astraspididae n. g., n sp. 1, Nr10-098, région du Morkoka Moyen (9 dans figure 1), sondage 151, profondeur 63,7 m., Ordovicien supérieur, horizon de Bura · B, Tesakoviaspis concentrica *Karatajute-Talimaa, Nr 10-099, région de Tchuna-Biriussa (6 dans figure 1), gisement du Vieux Balturino, couche 42, Silurien inférieur, Llandovery inférieur, sous-formation de Balturino inférieure ; C, D, Astraspididae n. g., n. sp. 2, Nr10-100 et 10-101, région entre les rivières Markha et Morkoka (9 dans figure 1), sondage 412, profondeur 315 m., Silurien inférieur, Llandovery inférieur ; E, F, Astraspidida ? n. g., Nr 10-102 et 10-103, région de Niuya-Beresovo (8 dans figure 1), rivière Niuya, gisement 157, couche 37, Silurien inférieur, Llandovery moyen, sous-formation de Utakan inférieure. Toutes les illustrations des tessères sont basées sur des spécimens immergés dans l'essence d'anis.*
Abrév. : pt, tubercule primordial ; t, tubercules des zones de croissance concentriques ; dt, tubules dans l'orthodentine ; pc, cavité pulpaire remplie d'ostéodentine (?).

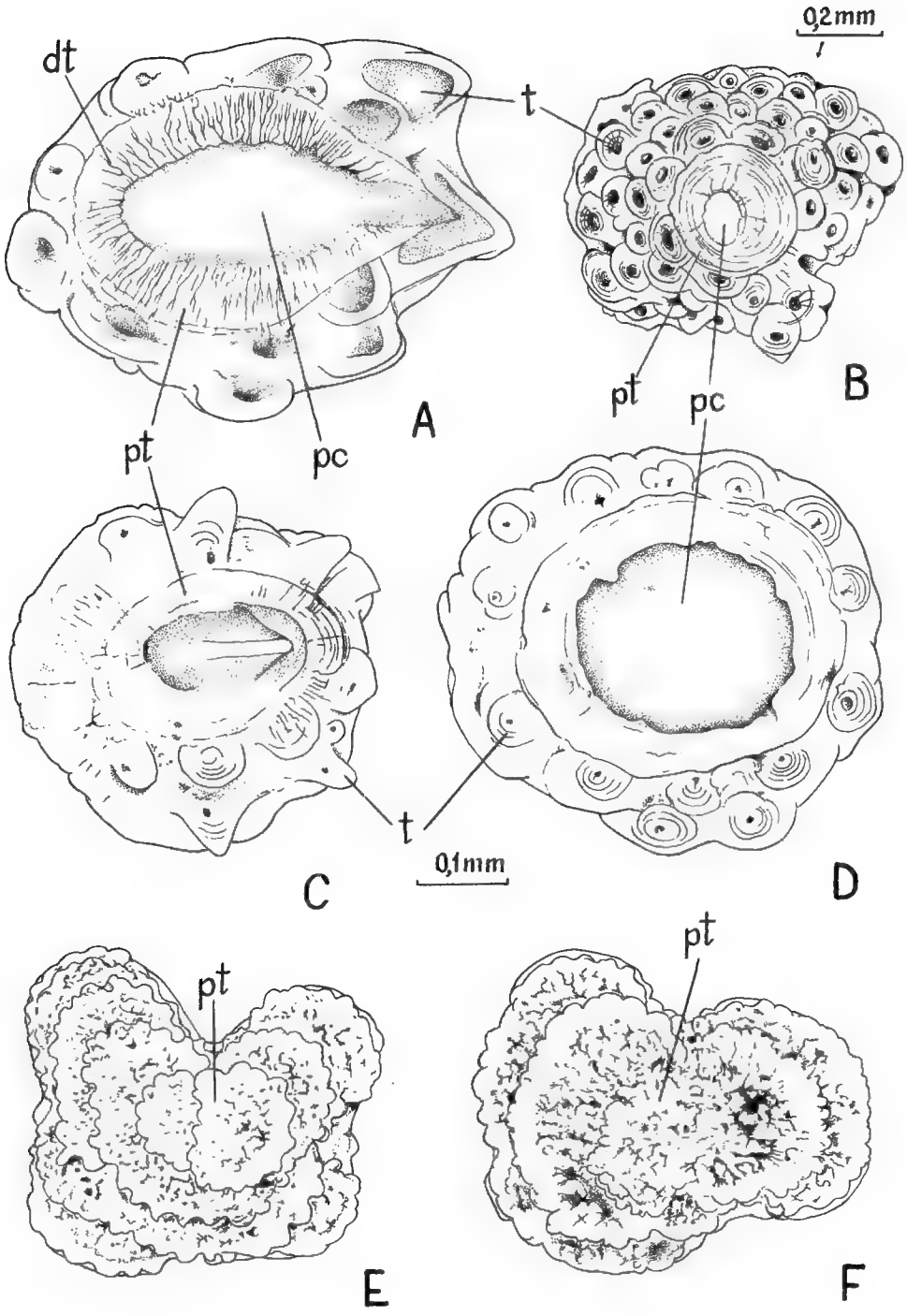

0,2mm
dt
t
pt
pc
A
B
pt
pc
C
D
t
0,1mm
pt
pt
E
F

Figure 7B illustrates a completely formed tessera of Astraspididae (*Tesakoviaspis concentrica* Karatajute-Talimaa, 1978), with the central, rounded tubercle, and four zones of areal growth consisting of rounded, very closely packed, tubercles. Clear growth lines and thin dentine tubules are visible in tubercles. The tesserae of Astraspididae n. g., n. sp. 2 (Fig. 7C, D) are characterized by large, rounded and flattened central tubercles (Fig. 7D), or more frequently, high, thorn-like ones (Fig. 7C), with comparatively small, scattered sharp-topped tubercles on the areal growth zones. In all astraspidids of this type, the pulp cavities of the tubercles are well developed, even in the smallest ones.

The structure found in the small tesserae of Astraspidida? n. g. (Fig. 7E, F) is entirely different. These elements show a central part, surrounded by concentric growth zones which generally do not form a full circle. The nature of the dentinous tissue which forms the crown of the tesserae is not very clear (it resembles somewhat osteodentine); it is a comparatively dense tissue, without distinct pulp cavities.

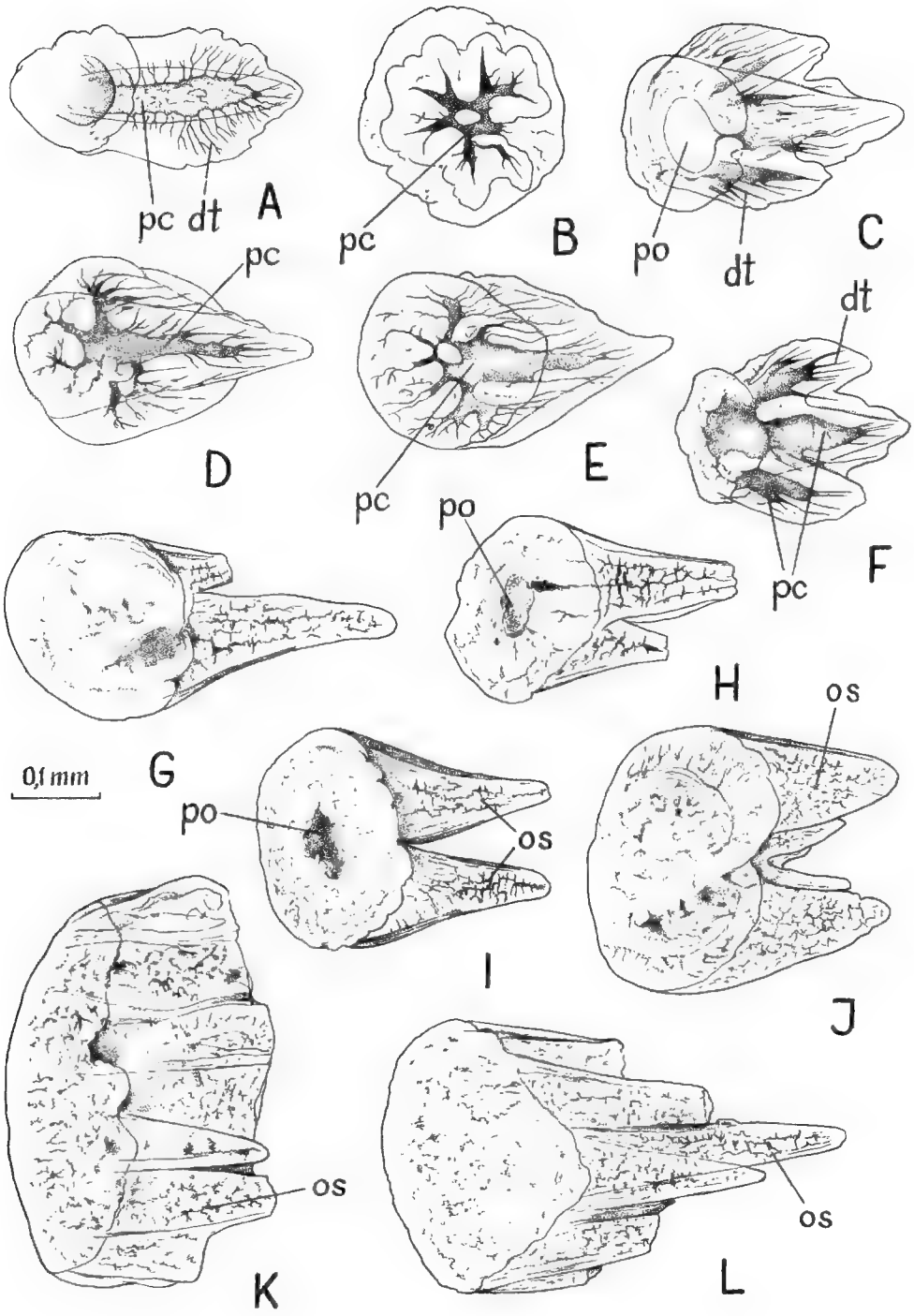
The thelodontid scale in Figure 8A has a high neck and a small, anteriorly protruding base; it resembles the scales of *Apalolepis* (KARATAJUTE-TALIMAA, 1978). The crown has one large pulp cavity with dentine tubuli branching off from it; the crown structure is characteristic of orthodentine. This scale belongs to the oldest representatives of the Thelodontida. Up to now, scales of a member of this order (*Thelodus* sp.) were known from the Upper Llandovery (TURNER, 1973; MÄRSS, 1986; TURNER, 1986). The majority of the thelodont scales found in the Lower Silurian of the Siberian Platform belong to the Loganiidae, but their generic and specific assignment deserves further clarification.

Chondrichthyans are an important component of the vertebrate assemblages of the Lower Silurian of the Central Asian region. At least three orders are represented, with forms which are differentiated mainly by their exoskeleton.

The body of elegestolepidids was covered with simple, non-growing shedding scales. Figure 8B-F shows the scales of *Elegestolepis conica* KARATAJUTE-TALIMAA (1986) to illustrate the variability of the scale morphology. There are rounded head scales with a low, flattened crown (Fig. 8B), and body scales, which are either single-topped with a high, conical crown and a unique pulp cavity (Fig. 8D, E) or three-topped with three pulp cavities (Fig. 8C, F). The dentinous tissue of the scale crowns is specific, whereas the dentine tubules in the superficial layers of the crown are characteristic of orthodentine.

FIG 8. — Thelodontid and elasmobranch scales. A. Thelodontida gen. indet., Nr 10-104, Niuya-Beresovo area (8 in Figure 1), Niuya River, outcrop 157, bed 30, Lower Silurian, Middle Llandovery, Lower Utakan Subformation; B-F, *Elegestolepis conica* Karatajute-Talimaa Nrs10-105 to 10-109, Niuya-Beresovo area (8 in Figure 1), Niuya River, outcrop 157, bed 30, Lower Silurian, Middle Llandovery, Lower Utakan Subformation; G-L, Elasmobranchii n. g., Nrs 10-110 to 10-115, Niuya Beresovo area (8 in Figure 1), Niuya River, outcrops 156 bed 37 (J, K, L) and 157 bed 37 (G, H, I), Lower Silurian, Middle Llandovery, Lower Utakan Subformation. All illustrations are based on scales immersed in aniseed oil.
Abbr.: po, pulp opening; pc, pulp cavity; dt, dentinal tubules; os, osteodentine?

Écailles de Thélodontides et Élasmobranches. A, Thelodontida gen. indet., Nr 10-104, région de Niuya-Beresovo (8 dans figure 1), rivière Niuya, gisement 157, couche 30, Silurien inférieur, Llandovery moyen, sous-formation de Utakan inférieure ; B-F, Elegestolepis conica *Karatajute-Talimaa, Nrs 10-105 à 10-109, région de Niuya-Beresovo (8 dans figure 1), rivière Niuya, gisement 157, couche 30, Silurian inférieur, Llandovery moyen, sous-formation de Utakan inférieure ; G-L, Elasmobranchii n. g., Nrs 10-110 à 10-115, région de Niuya-Beresovo (8 dans figure 1), rivière Niuya, gisement 156, couche 37 (J, K, L) et gisement 157, couche 37 (G, H, I), Silurien inférieur, Llandovery moyen, sous-formation de Utakan inférieure. Toutes les illustrations sont basées sur des écailles immergées dans l'essence d'anis.*
Abrév. : po, ouverture pulpaire ; pc, cavité pulpaire ; dt, tubules de la dentine, os, ostéodentine ?


pc
dt
A
pc
B
po
dt
C
pc
D
pc
E
dt
pc
F
po
H
G
0,1 mm
po
os
I
os
J
os
K
os
L

A completely different dentine type has been found in the scale crowns of the Elasmobranchii n. g. (Fig. 8G-L). It may resemble osteodentine by the arrangement of the short dentine tubules and the presence of small cavities between them. In some cases the bicuspidate crowns of these scales have a single pulpar opening (Fig. 8H, J), whereas in the other cases every crown cusp has its individual pulpar opening. Evidently, this type of scale is representative of a new elasmobranch genus characterized by a synchronomorial type of growth.

The scale structure in mongolepidid chondrichthyans is rather complex (KARATAJUTE-TALIMAA *et al.*, 1990). The odontodes forming the scale crowns are arranged into longitudinal rows and are fused into complicated odontocomplexes. The odontodes consist of a specific atubular dentine referred to as lamelline. The scale crowns had a synchronomorial mode of growth.

Acanthodians are abundant in the biocoenoses of the Early Silurian paleobasin of the Siberian Platform, beginning with the Late Llandovery. In the Upper Llandovery, the scales of Acanthodii n. g. B predominate among microremains in almost every sample. The head scales of this form resemble the elasmobranchs scales of the *Holmesella* type by their more of growth. The layers of bone tissue grow superpositionally only on the sides and downwards around the primordial scale, and do not cover the upper parts of the crown. Some of the transitional and body scales have a superpositional growth, as usual in acanthodian scales. All Early Silurian acanthodian of this region have a well developed bone tissue not only in the base, but also in the crown of the scales (mésodentine).

The study of the structure of the most common exoskeletal elements in the Upper Ordovician and Lower Silurian of the Siberian Platform leads to the conclusion that various types of ossification, growth, and hard tissues were present already at the beginning of the Early Palaeozoic.

- Accordingly the types of ossification are:

Two kinds of simple, non-growing monodontodia, respectively: 1) with one basal pulpar opening (Thelodontida); 2) with basal and neck pulpar openings (Elegestolepidida).

The polyodontodia, represented by: 1) simple scales formed by increment (adding) of new odontodes to the pre-existing ones (Elasmobranchii, n. g.); 2) scales consisting of a system of longitudinal odontocomplexes (Mongolepidida) and 3) odontocomplexes with concentric growth zones around the embryonic scale primordium (Acanthodii, lower Chordata?).

The tesserae (Astraspididae, Astraspidida?).

- The modes of growth include:

The cyclomorial areal growth (Astraspididae, Astraspidida?);
The areal superpositional growth directed toward the epithelium (Acanthodii);
The areal superpositional growth directed toward the korium (Acanthodii, lower Chordata?);
The synchronomorial growth (Elasmobranchii n. g., Mongolepidida).

- The types of tissues are:

Aspidin (acellular bone tissue; Astraspidida, Thelodonti, Elasmobranchii, lower Chordata?),
Bone with cell-spaces (Acanthodii);
Orthodentine (Astraspididae ?, Thelodontida, Elegestolepidida);

Osteodentine ? – (Astraspidida? n. g., Elasmobranchii n. g.);
Mesodentine-like ? tissue (Thelodonti, Loganiida);
Lamelline or atubular dentine (Mongolepidida).

Taking into account an enormous variety in the structure of the exoskeleton of the earliest vertebrates, it is difficult to consider one of the tissue or growth types mentioned above as primitive. Evidently, the skin differentiation took place before the hard tissues appeared in them.

ADDENDUM

The three thinsections of *Tesakoviaspis concentrica* tesserae have been studied by help of the excellent microscope at the Department of Anatomy UM/DS Guy's Hospital, in London. It has turned out, that the tubercles of tesserae do not consist of orthodentine, as it has been assumed earlier, but of unusual atubular tissue, which has been called by us with Dr Moya M. Smith as "conical lamelline". Hence, the all tesserae, attributed by us to Astraspididae, Astraspidida or Astraspidida? (Figs. 3, 7), really are not Astraspides, but represent a new group of lower vertebrates with cyclomorial type of tesserae growth.

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Silurian and Devonian jawless craniates (Galeaspida, Thelodonti) and their habitats in China

by Nian-Zhong WANG

(A contribution to IGCP 328-Palaeozoic Microvertebrates and The National Science Foundation of China)

Abstract. — A review of fossil jawless craniate studies in China concerns mainly galeaspids and thelodonts. The pattern and structure of the sensory line system in galeaspids differs greatly from that of osteostracans or heterostracans. The order Macrothyraspidida is a monophyletic group within the Galeaspida, defined by an important synapomorphy, *i.e.* the cephalic shield with a pair of latero- or medial dorsal fenestrae. The habitat of fossil jawless craniates in China might have been littoral to neritic, on the basis of associated marine fossils and the analysis of fish-bearing sedimentary facies. They are considered to be euryhaline animals and not solely fresh water.

Keywords. — Galeaspida, Thelodonti, Silurian, Devonian, China, morphology, phylogeny, habitat.

Les Crâniates sans mâchoires du Siluro-Dévonien (Galeaspida, Thelodonti) et leurs habitats en Chine

Résumé. — Les recherches sur les Crâniates fossiles sans mâchoire en Chine concernent essentiellement les Galéaspides et les Thélodontes. Le trajet et la structure des lignes sensorielles chez les Galéaspides diffèrent remarquablement de ceux des Ostéostracés ou des Hétérostracés. L'ordre de Macrothyraspidida est un groupe monophylétique de Galeaspida caractérisé par une importante synapomorphie : le bouclier dorsal avec une paire des fenêtres latéro- ou mesio-dorsales. L'habitat des Galéaspides et des Thélodontes en Chine était principalement littoral à néritique, comme en témoignent les fossiles marins associés et l'analyse du faciès sédimentaire. Ils peuvent être considérés comme des animaux euryhalins et non pas uniquement d'eau douce

Mots-clés. — Galeaspida, Thelodonti, Silurien, Dévonien, Chine, morphologie, phylogénie, habitat.

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INTRODUCTION

The studies of fossil jawless craniates (Agnatha) in China can be divided into four periods: the 1930-1940s, 1960s, 1970s and the last ten years.

Agnathans were first reported from South China in 1937 by TING V.K. & WANG Y.L. At the 18th International Geological Congress, YOUNG C.C. (1951) recorded the Devonian vertebrates including "*Cephalaspis*". This material was never described. However, in the same area (Qujing, Yunnan Province) and same horizons within the Cuifengshan Group, several peculiar agnathans were discovered during the early 1960s. The new genera *Eugaleaspis* (*Galeaspis*) and *Nanpanaspis* were assigned to the Osteostraci (Cephalaspides), while *Polybranchiaspis* was

placed in the Heterostraci (Pteraspides) (LIU, 1965). These fossils were unlike any previously described jawless craniates and their relationship to the known major groups became a subject of controversy. TARLO (1967) suggested that eugaleaspids (galeaspids) and polybranchiaspids should be united into a higher category, the Galeaspida, on the basis of the shape of the dorsal shield, and classified among the Cephalaspidomorphi, with the same rank as the Osteostraci, Anaspida, and Petromyzontida. This view was supported by JANVIER (1975) but was rejected by MOY-THOMAS & MILES (1971). This view received the support from Chinese paleontologists in the early 1980s (WANG & WANG, 1982a; ZHANG *et al.*, 1986).

In the 1970s many new galeaspid genera of Early Devonian age from Yunnan, Guangxi, Sichuan and Guizhou provinces were described (LIU, 1975; PAN *et al.*, 1975; PAN & WANG, 1978) and were classified with the heterostracans. By that time it was clear that South China was a unique vertebrate province where fossil jawless craniates underwent a great radiation.

In the last decade, research work has greatly expanded and previous work on jawless craniates has been confronted by a serious challenge in several aspects.

ABBREVIATIONS

bo	buccal opening, *ouverture buccale*;
bro	branchial opening, *ouverture branchiale*;
dbo	"dorso-branchial openings", "*ouvertures branchiales dorsales*";
ldo	latero-dorsal fenestrae, *fenêtres latéro-dorsales*;
no	exonasal openings, *ouvertures nasales externes*;
orb	orbital openings, *orbites*;
pdo	medial dorsal fenestrae, *fenêtres mésio-dorsales*;
pi	pineal opening, *ouverture pinéale*;
scs	sensory canal system, *système des canaux sensoriels*;
sis	sensory line system, *système de la ligne sensorielle*;
Vp	ventral plate, *plaque ventrale*;
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica;
MGB	Museum of Geology, Beijing.

REVIEW OF THE FOSSIL JAWLESS CRANIATE STUDIES IN CHINA

First many new galeaspid genera have been described not only from the Early Devonian strata of the southwestern provinces but also the Early Silurian strata in the region of the middle and lower reaches of the Yangtze River (PAN & WANG, 1981; WANG & WANG, 1982a, 1982b; WANG, 1984, 1986b, 1991; LIU, 1985; PAN & DINELEY, 1988; ZHU, 1992; WANG & WANG, 1992; PAN & CHEN, 1993). The new fossils of Early Silurian galeaspids found in Northwest China (Kalpin District, Xinjiang) are very similar to those of *Hanyangaspis* from Hubei Province of South China. This has important biogeographic significance because it suggests that the Tarim Block and the South China Block have a more close relationship than other blocks in the Early Silurian period (Fig. 1).

Second, the data on the external characters of the Galeaspida are fairly complete. The Galeaspida possess a bony cephalic shield, varying both in shape and size and covering the

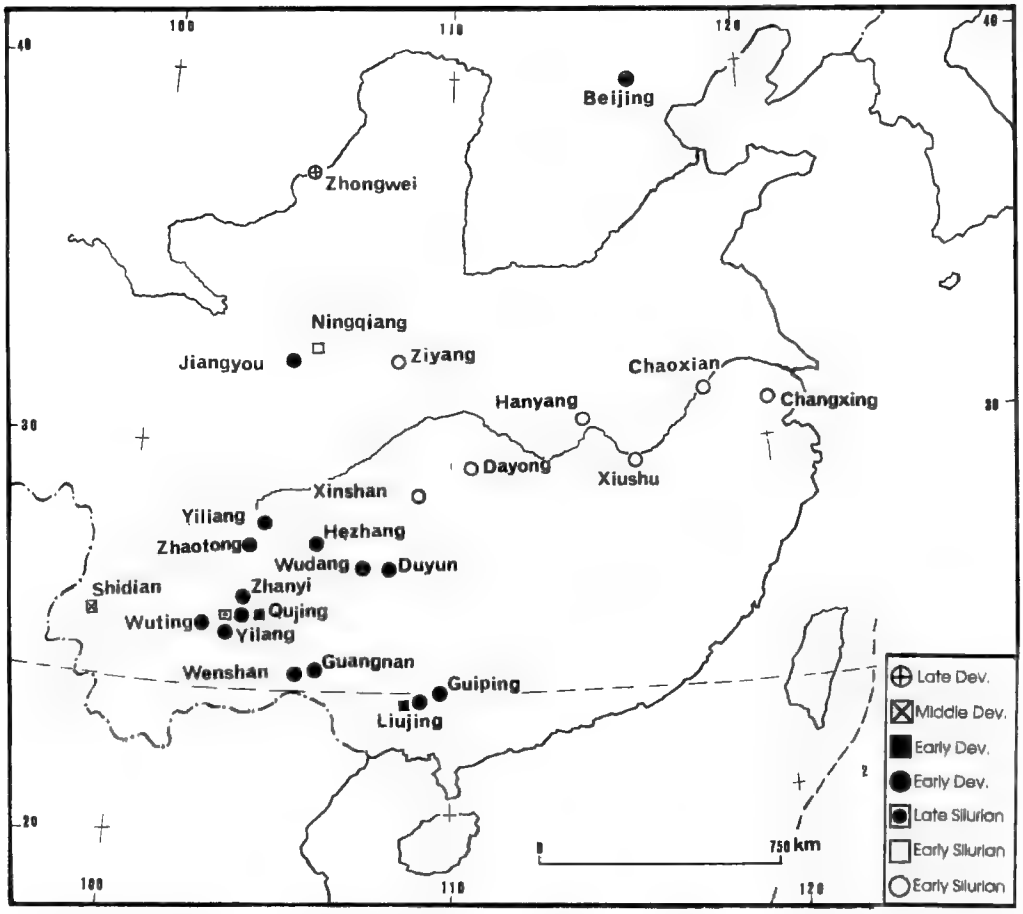


FIG. 1. — Localities of Silurian and Devonian Galeaspida and Thelodonti in China. Round marks: Galeaspida, square marks: Thelodonti.

Localités à Galéaspides et Thélodontes siluriens en Chine. Marques rondes : Galéaspides, carrés : Thélodontes.

anterior part of the body. In some forms there is a cephalic shield with a long rostral process, and long lateral or posterior, cornual processes (Fig. 2H, I). The dorsal part of the cephalic shield consists of a single exoskeletal plate, commonly with a large opening for the exonasal openings, paired orbital openings, a single pineal opening and in some forms even paired latero– or medio dorsal fenestrae (Fig. 2I) and with a galeaspid-type sensory canal system. The ornament consists of snowflake-shaped tubercles.

There are two types of ventral part of cephalic shield : one is found in *Hanyangaspis* (Fig. 2B) and *Pentathyraspis*, the former with both anteroventral and posteroventral plates and the latter with only one ventral plate covering completely the orobranchial chamber, and with a buccal opening and paired, separate, pore-like branchial openings. The other type is that of

Polybranchiaspis (Fig. 2F), with a median ventral plate and peripheral tesserae, a buccal opening, and many, paired, individual branchial openings.

There are narrow and deep lateral scales. In some forms there are dorsal ridge scales, and small diamond-shaped scales on the ventral surface of the tail. There is no evidence of movable paired fins and *Sanqiaspis rostrata* had a hypocercal tail (HALSTEAD *et al.*, 1979).

Third, several specimens of Galeaspida from both the Lower Devonian and Lower Silurian of China show internal anatomy, including the central nervous system, vascular system and various sensory organs, preserved as internal casts. Examples include *Duyunolepis* (*Duyunaspis*) and *Paraduyunaspis* (PAN & WANG, 1978); in particular, the internal anatomy of *Changxingaspis* (WANG, 1991) is extremely well preserved. A summary of the internal anatomical characters of the Galeaspida based mainly on specimens of *Changxingaspis gui* is given in Figure 3, (also see WANG, 1991, pls 1C, D, 2B, 3, 4, 5B).

Five divisions of the cranial cavity can be recognized: telencephalic, diencephalic, mesencephalic, metencephalic and myelencephalic. Nine pairs of cranial nerve canals have been identified: terminal, olfactory, optic, oculomotor, trochlear, trigeminal, facial, glossopharyngeal and vagus nerves. Of these, the structure of the telencephalic portion and the long terminal and olfactory nerves are very important for deciding the phylogenetic relationship of the Galeaspida.

The most prominent feature of the vascular system is the paired lateral head veins, a large dorsal aorta, paired extrabranchial arteries and a subaponeurotic plexus in the cephalic shield.

The major features of galeaspid sensory organs were the separate, paired nasal sacs that lack an ossified floor; the single pineal and parapineal organ; the anterior and posterior vertical semicircular canals of the labyrinth cavity with ampullae, sacculus and endolymphatic duct opening externally. Among them, the structure of the separate, paired nasal sacs is important for deciding the phylogenetic relationship of the Galeaspida. In addition, six to more than twenty pairs of branchial pouches have separate openings to the exterior. A detailed histological study of the exoskeleton in the Galeaspida remains to be unraveled through good material (REIF, 1982; JANVIER, 1990; WANG, 1991).

Following on from the discovery of new forms and new characters of the Galeaspida, the discussion of the relationship between jawless craniates and the Gnathostomata has become focused on the position of the Galeaspida, which has changed substantially. HALSTEAD (1982) suggested a sister-group relationship between the Galeaspida and the Osteostraci, and also between the Heterostraci and the Gnathostomata. JANVIER (1984) showed a sister-group relationship between the Osteostraci and the Gnathostomata, while the Galeaspida were placed as the sister-group of the Osteostraci plus Gnathostomata. The author (WANG, 1991) pointed out a sister-group relationship between the Galeaspida and the Gnathostomata; in this case the Osteostraci should be placed as the sister-group of the Galeaspida plus Gnathostomata. A close relationship between osteostracans, galeaspids and gnathostomes has been proposed by YOUNG (1991, Fig. 8a), yet in an unresolved trichotomy. One functional interpretation of the galeaspid median dorsal opening has been given by BELLES-ISLES (1985), who regarded the opening as an exhalant one that permitted water to flow through the gills by the mechanism of fluid induction. In addition, the mould of four rows of high, narrow trunk scales has been found in China, and regarded as anaspid scales in China (LIU, 1983), but there is not the slightest evidence for the existence of either the Osteostraci or the Heterostraci in Silurian and Devonian strata of China (WANG, 1986b).

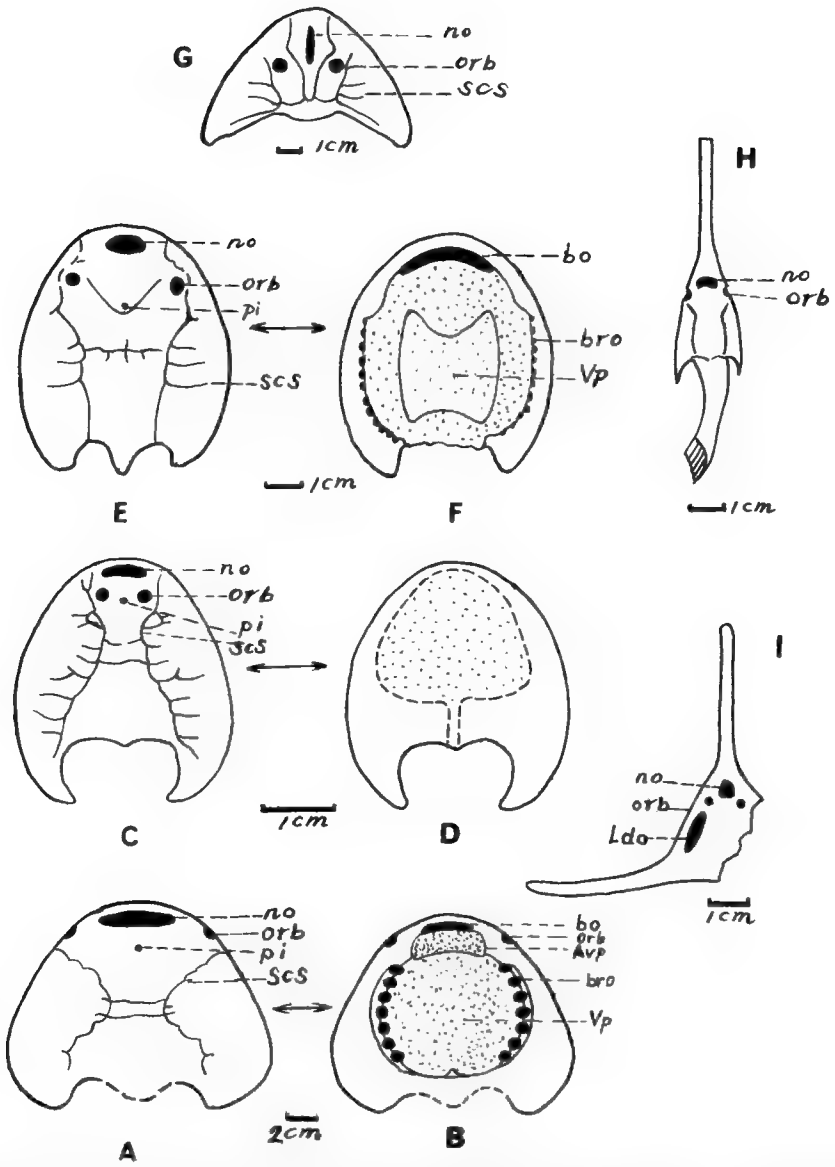


FIG. 2. — Main external characters of the Galeaspida. A, B, *Hanyangaspis guodingshanensis* (from WANG, 1986, Figs. 1,3). C, D, *Changxingaspis gui* (from WANG, 1991, Figs. 1,2). E, F, *Polybranchiaspis liaojiaoshanensis* (from LIU, 1975, Fig. 5A, B). G, *Eugaleaspis xujiachongensis* (from LIU, 1975, Fig. 2). H, *Sanqiaspis rostrata* (from LIU, 1975, Fig. 12). I, *Lungmenshanaspis kiangyouensis* (from WANG, 1991, Fig. 14). A, C, E, G-I, dorsal aspect; B, F, ventral aspect; D, extent of the endoskeleton (stipple).

Principaux caractères externes des Galeaspida. A, B, Hanyangaspis guodingshanensis *(d'après* WANG, *1986, figs 1, 3). C, D,* Changxingaspis gui *(d'après* WANG, *1991, figs 1, 2). E, F,* Polybranchiaspis liaojiaoshanensis *(d'après* LIU, *1975, fig. 5 A, B). G,* Eugaleaspis xujiachongensis *(d'après* LIU, *1975, fig. 2). H,* Sanqiaspis rostrata *(d'après* LIU, *1975, fig. 12). I,* Lungmenshanaspis kiangyouensis *(d'après* WANG, *1991, fig. 14). A, C, E, G-I, face dorsale ; B, F, face ventrale ; D, distribution de l'endosquelette (grisé).*

FIG. 3. — *Changxingaspis gui* (from WANG, 1991, Pl. 3) showing the neurocranium and visceral endoskeleton. IVPP V8297, 2. (Scale bar: 1 mm.)

Changxingaspis gui (d'après WANG, 1991, pl. 3) montrant le neurocrâne et l'endosquelette viscéral. IVPP V8297, 2. (Échelle : 1 mm.)

Fourth, Silurian and Devonian thelodonts have been recorded from China (WANG, 1984; WANG *et al.*, 1986; WANG & DONG, 1989; WANG, 1992) (Fig. 4). The diversity of the chinese fossil jawless craniates has been increased, since the group contains not only the endemic galeaspids, but also both cosmopolitan and endemic thelodonts (GROSS, 1967; KARATAJUTE-TALIMAA, 1978; TURNER, 1991; WANG, 1993). The thelodont from China currently consists of isolated scales from the Ludlow, Gedinnian, Emsian, Eifelian and Givetian of southwestern China. They are very useful for dating fish-bearing strata.

Turinia asiatica from the Xitun Formation of the Cuifengshan Group, Qujing District, Yunnan Province, is the first report of thelodonts in China (WANG, 1984). A new combined programme to recollect fossils bed by bed from the Cuifengshan Group was made in 1991, in which abundant thelodont scales were extracted by treatment with dilute acetic acid from the samples of 14 layers (YDC.59, YDC.145) in both the Xishancun and Xitun Formations of the Cuifengshan Group. A new genus, which consists of five species including four new ones and *Turinia asiatica*, will be erected, along with thelodontidae gen. indet. on the basis mainly of new material (WANG, MS.).

The lower part of the Cuifengshan Group was placed in the Early Devonian by many workers because of its endemic vertebrate content and its plant fossils. It was placed in the Pridolian by MU *et al.* (1986) although it does not have any fossils of proven Pridolian age, but only because it gradationally overlies Late Ludlow conodonts, the *crispus* zone (WANG, 1981) in the upper part of the Yulongsî (Yulungssu) Formation. I place the thelodont-bearing strata (the lower part of the Cuifengshan Group) in the Late Pridolian to Early Lochkovian on the basis of the new thelodont genus with the characters of both Silurian *Thelodus* and Devonian *Turinia* and the following arguments. The brachiopods fossils of the Miaogao (Miaokao) Formation, which conformably underlies the Yulongsi Formation, were regarded as Late Ludlovian to Early Pridolian age and those of the Yulongsi Formation as Pridolian (RONG & YANG, 1981). Recently, new conodont and chitinozoan assemblages were found in the uppermost part of the Yulongsi Formation in the Qujing area. The former includes *Ozarkodina excavata*, *Deutacodina* sp., and cf. *Ligonodina elegans detorta* overlying the *crispus* zone, in which *Ligonodina elegans detorta* is the uppermost zone fossil of the Pridolian. The latter includes *Eisenackitina*, *Lagenomorpha* and *Margachitina* sp. belonging to the *Margachitina elegans* zone of Middle Pridolian age (CAI *et al.*, 1994). A more important argument is that a species of the new thelodont genus in the Cuifenshan Formation, in conjunction with conodont *Icriodus woschmidti*, was found in the lower Putonggou Formation of Early Lochkovian age in the West Qinling Mountains, Gansu Province, North China (WANG *et al.*, MS.).

Thelodus sinensis from the Guandi (Kuanti) Formation and *Kawalepis comptus* from the Miaogao Formation of Qujing, Yunnan, were regarded originally as two Ludlovian thelodonts (WANG & DONG, 1989), but the latter may be a palaeoniscoid scale (ESIN & TALIMAA, pers. comm.).

Turinia sp. and Nicoliviidae gen. indet. are two isolated thelodont scales from the Emsian Yukiang Formation, Liujing area, central Guangxi (WANG, 1992).

Turinia pagoda from the Givetian Heyuanzhai Formation, *Turinia* n. sp.? A and *Turinia* n. sp.? B from the Eifelian Malutang Formation were discovered in Shidian County, West Yunnan (WANG *et al.*, 1986). The former may be regarded as a new genus within thelodontidae (TALIMAA pers. comm.).

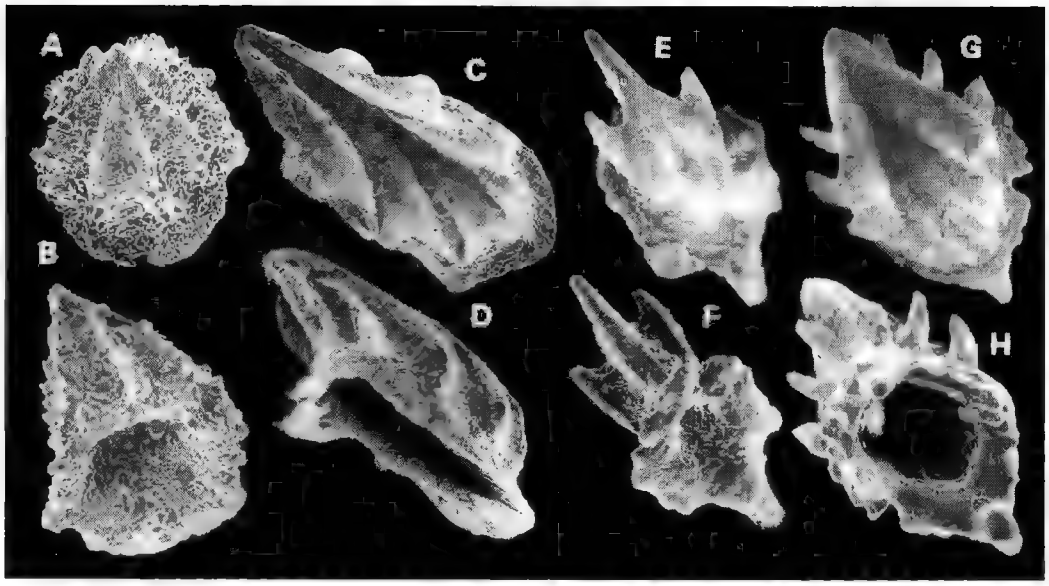


FIG. 4. — A, B. *Thelodus sinensis*, a thelodont scale from the Guandi Formation (Ludlow-Pridoli) of the Qujing area, Yunnan Province (from WANG & DONG, 1989, Pl.1F, G). IVPP V7225. 1 (×50). C, D. *Turinia* sp., a thelodont scale from the Yujiang Formation (lower Emsian) of the Liujing area, Guangxi Province (from WANG, 1992, Pl. 1A-B), IVPP V9743 (×50). E, F. *Turinia* sp. nov.? B, a thelodont scale from the Malutang Formation (Middle Devonian) of the Shidian County, West Yunnan (from WANG *et al.*, 1986, Fig. 6G-H), IG-VF357 (×60). G, H. *Turinia pagoda*, a thelodont scale from the Heyuanzhai Formation (Middle Devonian) of the Shidian County, West Yunnan (from WANG *et al.*, 1986, Fig. 6A-B), IG-VF356 (×42). A, C, E, G, external view; B, D, F, H, basal view.

Thelodus sinensis. *une écaille de thélodonte de la Formation de Guandi (Ludlow-Pridoli) de la région de Qujing, Yunnan (d'après* WANG & DONG, *1989, pl. 1F, G), IVPP V7225. 1 (× 50) ; C, D.* Turinia *sp., une écaille de thélodonte de la Formation de Yujiang (Emsien inférieur) de la région de Liujing, Guangxi (d'après* WANG, *1992, pl. 1A, B), IVPP V9743 (× 50). E, F.* Turinia *sp. nov.? B, une écaille de thélodonte de la Formation de Malutang (Dévonien moyen) du district de Shidian, Yunnan occidental (d'après* WANG et al., *1986, fig. 6G-H), IG-VF357 (× 60). G, H.* Turinia pagoda, *une écaille de thélodonte de la Formation de Heyuanzhai (Dévonien moyen) du district de Shidian, Yunnan occidental (d'après* WANG et al., *1986, fig. 6A-B), IG-VF356 (×42). A, C, E, G, vue externe ; B, D, F, H, vue basale.*

THE SENSORY LINE SYSTEM IN THE GALEASPIDA

The dorsal part of the galeaspid cephalic shield displays the typical galeaspid pattern of the sensory line system. This pattern consists of three main elements: the supraorbital line, infraorbital line (latero-longitudinal line and latero-transversal lines), and one or two medio-transversal commissures. There are three major types of pattern:

1) supraorbital sensory-lines undeveloped or absent, two medio-transversal commissures, as in *Hanyangaspis* (Fig. 2A) and *Changxingaspis* (Fig. 2C);

2) a V-shaped pineal line and one medio-transversal commissure such as Huananaspiformes and *Polybranchiaspis*-like forms (Fig. 2E);

3) the pineal line extending backwards to contact with the medio-transversal commissure such as in *Eugaleaspis* (Fig. 2G). This sensory line pattern differs greatly from that of the Osteostraci or the Heterostraci (Fig. 5).

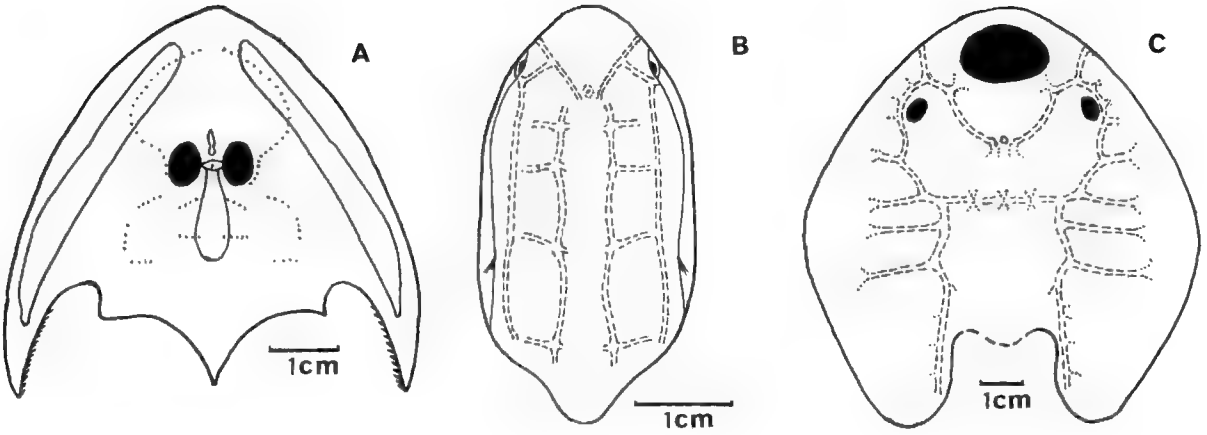


FIG. 5. — Pattern of sensory-line system in the dorsal shield. A, the osteostracan *Cephalaspis pagei* (slightly modified from STENSIÖ, 1932, Fig. 33A). B, the heterostracan *Poraspis* sp. (slightly modified from DENISON, 1964, Fig. 91A). C, the galeaspid *Damaspis vartus* (from WANG & WANG, 1982b, Fig. 1).

Répartition du système sensoriel de la ligne latérale sur le bouclier dorsal. A, l'Ostéostracé Cephalaspis pagei *(d'après STENSIÖ, 1932, fig. 33A, légèrement modifié). B, l'Hétérostracé* Poraspis *sp. (d'après DENISON, 1964, fig. 91A, légèrement modifié). C, le Galéaspide* Damaspis vartus *(d'après WANG & WANG, 1982b, fig. 1, légèrement modifié).*

Generally, the Osteostraci lack the supraorbital line and has an infraorbital line without latero-transversal lines. The Heterostraci have two paired, dorsal longitudinal lines joined into a separate dorsal network by transverse commissures (latero-transversal line).

The sensory-line system in the dorsal shield of the Galeaspida is well developed in the form of canals in the bony exoskeleton and superficial grooves (Fig. 6). It is connected with the *lateralis* nerve canals in the carapace by the pores situated in the lower part of the sensory canal. The pattern of the galeaspid sensory lines differs thus from that of the Osteostraci or the Heterostraci.

The sensory-line system of the Osteostraci is not embedded in the bony exoskeleton, but merely leaves a few fragmentary interrupted superficial grooves to indicate its course. The sensory-line system of the Heterostraci is well developed in the form of canals in the middle layer of the exoskeleton, which open to the exterior by a series of pores (STENSIÖ, 1932; DENISON, 1964; STENSIÖ, 1964; MOY-THOMAS & MILES, 1971; RITCHIE & GILBERT-TOMLINSON, 1977; JARVIK, 1980; NOVITSKAYA, 1983; BLIECK, 1984; JANVIER, 1985a). The Galeaspida resemble more the Heterostraci than the Osteostraci in the structure of sensory line system of the dorsal shield. This is probably a symplesiomorphy.

GALEASPIDS WITH THE PAIRED LATERAL OR MEDIAL DORSAL FENESTRAE

The plates and figures of three formerly described galeaspid genera attracted my attention. These are *Lungmenshanaspis* and *Sinoszechuanaspis*, both from the middle part of the Pingyipu

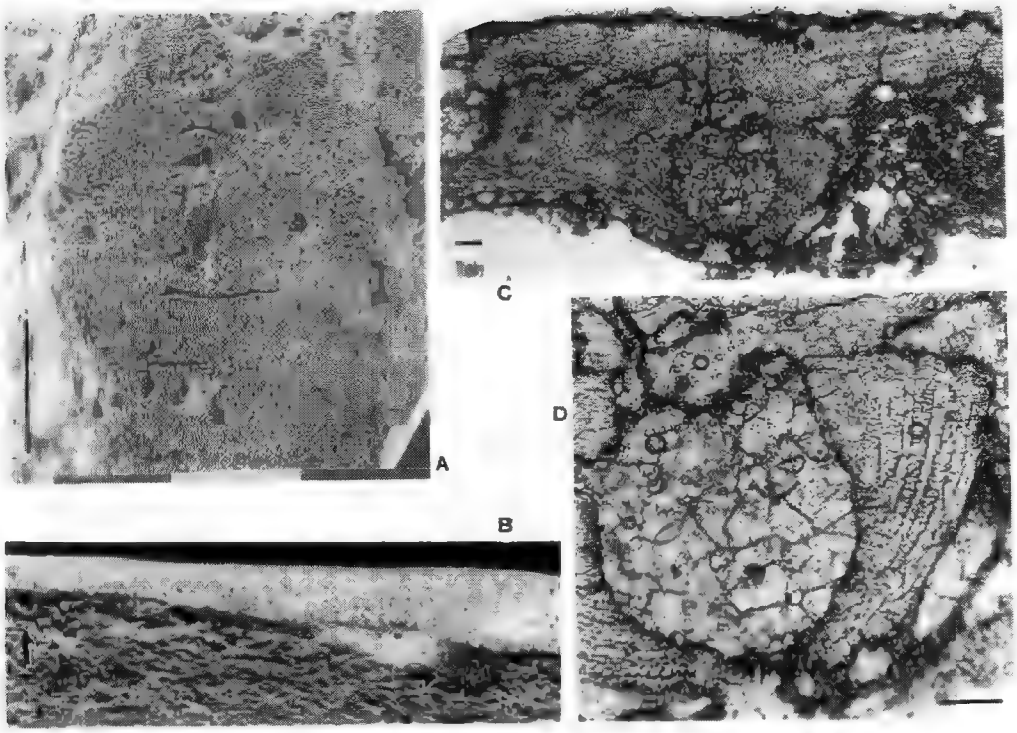


FIG. 6 — *Polybranchiaspis* sp., IVPP V10331. A, aspect of the canals and grooves of the sensory-line system of the dorsal shield (scale bar: 1 cm). B, vertical section of two canals (scale bar: 10 µm arrows). C, vertical thin section showing details of a canal (scale bar: 10 µm). D, vertical thin section showing the structure of the sensory canal wall and a passage between the sensory-line in the exoskeleton and the underlying cartilage (scale bar: 10 µm).

Polybranchiaspis sp., *IVPP V10331. A, aspect des canaux et sillons du systeme de la ligne latérale sur le bouclier dorsal (échelle. 1 cm). B, section vertirale de deux canaux (échelle : 10 µm flèches). C, section verticale d'un canal, montrant les détails de la structure (échelle : 10 µm). D, section verticale d'un canal montrant les détails de la structure des parois, ainsi qu'un passage entre le canal et l'endosquelette sous-jacent (échelle : 10 µm).*

Group, Lower Devonian, Jiangyou District of Sichuan Province (PAN *et al.*, 1975), and *Qingmenaspis* from the upper part of the "Cuifengshan" Group of Early Devonian age in the Qingmen area, Zhaotong District of Yunnan Province (PAN & WANG, 1981 and also see Fig. 7).

Previously, the author provided a new interpretation and a new illustration of the dorsal surface of a cephalic shield of *Lungmenshanaspis* (Fig. 8B) and considered *Lungmenshanaspis* to have paired latero-dorsal fenestrae (openings) of unknown function, judging by its plates (WANG, 1991).

In the original illustration of *Qingmenaspis*, a pair of openings in the dorsal shield was interpreted as "dorso-branchial openings" (PAN & WANG, 1981, Fig. 3 and also see Fig. 8F), which, in my opinion, is a pair of medial dorsal fenestrae (postero-dorsal openings) (Fig. 8G), and is a synapomorphy shared by *Qingmenaspis* and *Lungmenshanaspis* (WANG, 1991, Fig. 14).

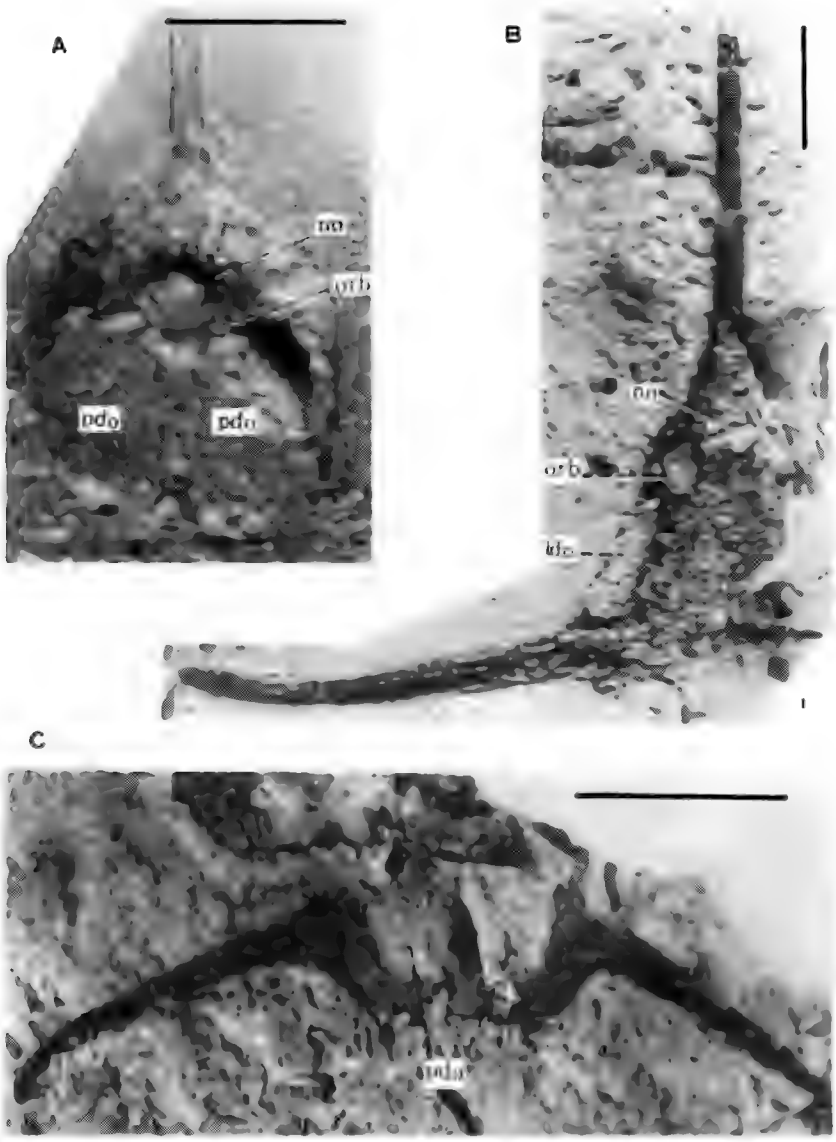


FIG. 7 — A. *Qingmenaspis microcelus* (from PAN & WANG, 1981, Pl. 1, Fig. 3), dorsal shield, MGB V1745. B. *Langmenshanaspis kiangyouensis* (from PAN *et al.*, 1975, Pl. 17, Fig. 1), dorsal shield, MGB V1513. C. *Sinozechuanaspis yanmenpaensis* (from PAN *et al.*, 1975, Pl. 2, Fig. 1), posterior part of the dorsal shield, MGB V1514. Scale bar: 1 cm.

A. Qingmenaspis microcelus *(d'après* PAN & WANG, *1981, pl. 1, fig. 3), bouclier dorsal, MGB V1745. B.* Langmenshanaspis kiangyouensis *(d'après* PAN et al., *1975, pl. 17, fig. 1), bouclier dorsal, MGB V1513. C.* Sinozechuanaspis yanmenpaensis *(d'après* PAN et al., *1975, pl. 2, fig. 1), partie postérieure du bouclier dorsal, MGB V1514. Échelle : 1 cm.*

In the original description of *Sinoszechuanaspis* (*Szechuanaspis*), a peculiar sensory line canal system in the dorsal shield was noted by PAN & WANG (1975, Fig. 3 and also see Fig. 8C). In the second illustration of the same specimen, the sensory line canal system was changed into a pattern with a pair of elliptic circles (PAN & DINELEY, 1988, Fig. 9, and also see Fig. 8D). Recently, PAN (1992) accepted the interpretation that the paired elliptical "sensory line system" are a pair of dorsal fenestrae (medial dorsal fenestrae in this paper) as true (Fig. 8E). I agree with this. A new genus, *Macrothyraspis*, described by PAN proved that the paired dorsal fenestrae exist in galeaspids.

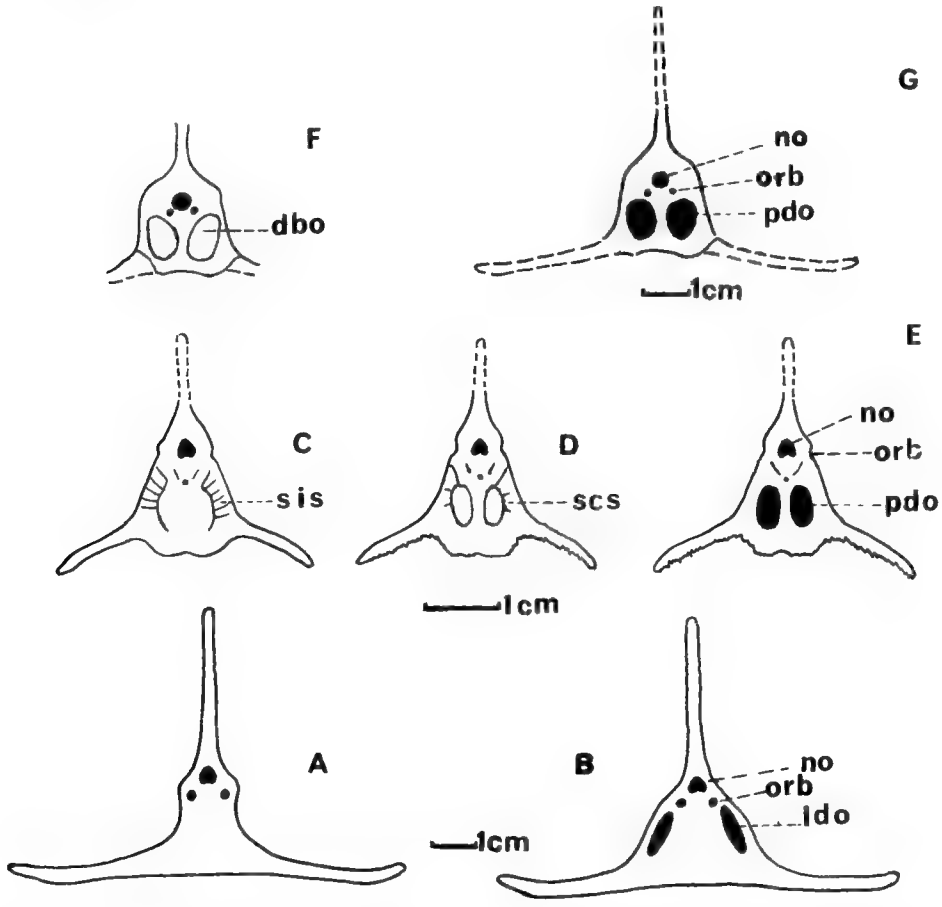


FIG. 8. — Different restorations of the dorsal shield in three genera of the Macrothyraspidida. A, B, *Lungmenshanaspis kiangyouensis*; C-E, *Sinoszechuanaspis yanmenpaensis*; F, G, *Qingmenaspis microculus*. A, C, from PAN *et al.*, 1975, Figs. 1, 4; B, from WANG, 1991, Fig. 14; D, from PAN & DINELEY, 1988, Fig. 9; E, G, slightly modified from PAN, 1992, Figs. 29, 30; F, from PAN & WANG, 1981, Fig. 3.

Différentes reconstitutions du bouclier dorsal chez trois genres de Macrothyraspidida. A, B, Lungmenshanaspis kiangyouensis ; *C-E,* Sinoszechuanaspis yanmenpaensis ; *F, G,* Qingmenaspis microculus. *A, C, d'après* PAN et al., *1975, figs 1, 4 ; B, d'après* WANG, *1991, fig. 14 ; D, d'après* PAN & DINELEY, *1988, fig. 9 ; E, G, légèrement modifié d'après* PAN, *1992, figs 29, 30 ; F, d'après* PAN & WANG, *1981, fig. 3.*

There are therefore four genera: *Lungmenshanaspis, Qingmenaspis, Sinoszechuanaspis* and *Macrothyraspis* all having paired lateral or medial dorsal fenestrae of unknown function, and a long rostral process, as well as a pair of long transverse cornual processes.

PAN (1992) described two other new genera: *Pentathyraspis* and *Microhoplonaspis*, bearing latero-dorsal fenestrae, but neither with a long rostral process nor a pair of long transversal cornual processes.

LIU (1993) compared the lateral fields of osteostracans with the lateral fenestrae (the lateral or medial dorsal fenestrae in this paper) of galeaspids. He thinks that "the lateral fenestrae of galeaspids are not only morphologically comparable with, but also phyletically homologous to the lateral fields of osteostracans, and the feature is shared only by osteostracans and galeaspids within agnathans".

The homology of the paired lateral or medial dorsal fenestrae in some galeaspids is a very interesting problem, I shall give my interpretation below.

First, the cephalic shield of osteostracans have one or more pairs of lateral fields and a single median field, but those of galeaspids possess only a pair of either latero-dorsal fenestrae or medial dorsal fenestrae.

Second, the paired lateral fields of osteostracans are situated laterally, in front of, and behind the orbital plane. On the contrary, a pair of latero-dorsal fenestrae as well as medial dorsal fenestrae of galeaspids are always situated always behind the orbital level. Moreover, the paired medial dorsal fenestrae of galeaspids are so large that they occupy most of the postero-dorsal part of the cephalic shield.

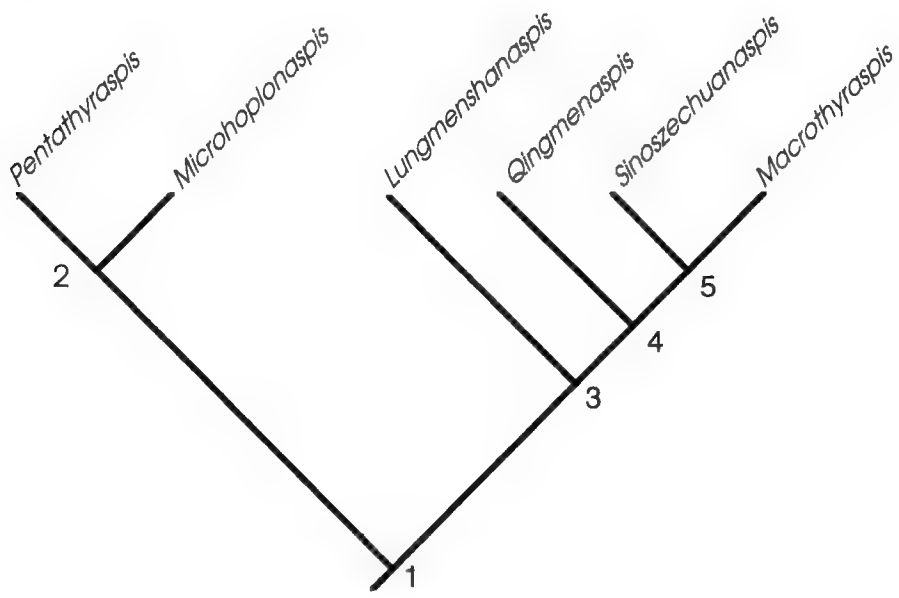


FIG. 9. — Phylogenetic interrelationships among the Macrothyraspidida.

Relations phylogénétiques entre les Macrothyraspidida.

Third, the lateral fields of osteostracans are covered with dermal platelets and are connected by canals to the capsule, whereas the latero– or medial dorsal fenestrae of galeaspids are devoid of any similar dermal platelets and canals.

Under such circumstances, it is difficult to say that the latero– or medial dorsal fenestrae of galeaspids are comparable both morphologically and homologically with the lateral fields of osteostracans. I think that the fenestrae are a synapomorphy of the fenestrate galeaspids and the order Macrothyraspidida is a monophyletic group within the Galeaspida. Six genera possessing the latero- or medial dorsal fenestrae can be referred to two families, the Macrothyraspididae and Pentathyraspididae. within the order Macrothyrasidida. The Macrothyraspididae includes four genera: *Lungmanshanaspis*, *Qingmenaspis*, *Sinoszechuanaspis* and *Macrothyraspis*, and the Pentathyraspididae includes two genera: *Pentathyraspis* and *Microhoplonaspis*. Their phylogenetic relationships are shown in the cladogram in Figure 9. The numbered synapomorphies are:

1. Dorsal shield with a pair of lateral or medial dorsal fenestrae placed behind the orbital level.

2. Cephalic shield with a pair of broad inner cornua.

3. Cephalic shield with a rostral process and a pair of long lateral cornual processes.

4. Dorsal shield with paired medial dorsal fenestrae.

5. A heart-shaped exonasal opening, orbital openings placed laterally.

It is interesting that the combination of a longitudinal slit-shaped exonasal opening and the eugaleaspid pattern of the sensory-line system used previously as the apomorphic characters for the Eugaleaspidiformes actually appear in the huananaspidid-like forms such as *Pterogonaspis*

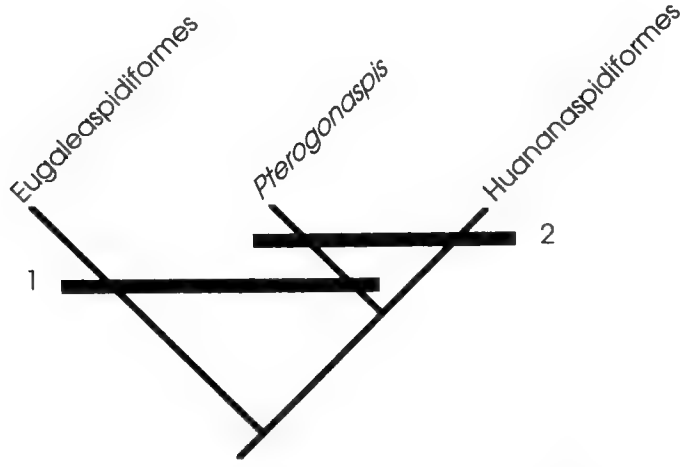


FIG. 10. — Cladogram showing the relationships between the Eugaleaspidiformes, Huananaspidiformes, and *Pterogonaspis*.
Cladogramme montrant les relations phylogénétiques entre les Eugaleaspidiformes, Huananaspidiformes, et Pterogonaspis.

(ZHU, 1992) and *Tridensaspis* (LIU, 1986). Similarly, the feature of the paired lateral or medial dorsal fenestrae is reported from the fenestrate huananaspidid-like forms (Macrothyraspididae) and in the polybranchiaspidid-like forms (Pentathyraspididae).

On account of the reason stated above, I consider that both the Huananaspidiformes and Eugaleaspidiformes, regarded previously as two monophyletic groups within the Galeaspida, are confronted by a serious challenge. I provide a cladogram showing this relationship (Fig. 10); the numbered synapomorphies are:

1. Longitudinal slit-shaped exonasal opening and supraorbital sensory lines in contact with the medial transversal commissure.

2. Cephalic shield with a long rostral process and a pair of long lateral cornual processes.

HABITAT OF THE FOSSIL JAWLESS CRANIATES (GALEASPIDS, THELODONTS) IN CHINA

The habitat of the fossil jawless craniates is a very interesting problem (ROBERTSON, 1957; ALLEN & TARLO, 1963; BOUCOT & JANIS, 1983; GOUJET, 1984; WANG, 1984, 1986b; HALSTEAD, 1985; JANVIER, 1985b; MÄRSS, 1991). The fossil jawless craniates found in China are represented by two groups: the Galeaspida and Thelodonti.

Most thelodonts have been extracted from Silurian and Devonian carbonates, particularly from bioclastic limestone, non-bioherm limestone and pseudo-oolitic limestone in China. *Thelodus sinensis* from the Late Ludlow to Pridoli Miaogao and Guandi Formations of Qujing District, Yunnan Province (WANG & DONG, 1989); *Turinia* sp. and Nikoliviidae gen. et sp. indet. from the Early Emsian Yujiang Formation of Liujing village, Guangxi Province (WANG, 1992); *Turinia* sp. nov.? A and *Turinia* sp. nov.? B from the Eifelian Malutang Formation and *Turinia pagoda* from the Late Givetian Heyuanzhai Formation of Shidian District of west Yunnan (WANG *et al.*, 1986). Associated fossils are conodonts, and other microfossils found mainly in shallow marine environment. The thelodonts were extracted from a marl and calcareous sandstone in the Xitun Formation of the Cuifengshan Group (WANG, 1984; WANG, MS). Other associated vertebrates are galeaspids, acanthodians, sarcopterygians, placoderms, chondrichthyans (WANG, 1984; ZHANG *et al.*, 1986) and marine bivalves, chitinozoans, acritarchs, inarticulate brachiopods, lingulids etc. (PAN *et al.*, 1978; FANG *et al.*, 1985). The thelodont-bearing strata indicate a littoral environment, judging from abundant chondrichthyan remains, marine invertebrates, and even other marine microfossils. Consequently, the thelodonts found in Silurian and Devonian strata of China occupied a littoral or neritic depositional environment.

The major question to be answered is: did the Galeaspida inhabit a marine or fresh water environment? The question can be answered on the basis of three sets of evidence.

1) Other fossils found with them in the Cuifengshan Group of Qujing, Yunnan;

2) the sedimentological analysis of galeaspid-bearing environments of the Lower Devonian in Sichuan, Guangxi and Guizhou Provinces;

3) the data of the Silurian galeaspids and galeaspid-bearing red clastic rocks.

The name of the Cuifengshan Group was derived from Mount Cuifeng located 10 km west of Qujing City, eastern Yunnan. According to the paleomagnetic data studied by C. LIU & Q.-Z. LIANG (in FANG *et al.*, 1985), the Qujing region was situated slightly north to the equator in Early Devonian times. The Lower Devonian section extends approximately 7 km from Xishancun village through the Xitun, Guijiatun to Xujiachong villages. Its thickness is 2100 m. It has good exposure, with abundant early vertebrate fossils, the first galeaspid fossil was recorded in this section. The Cuifengshan Group was regarded as continental for a long time because of its fresh water fishes and plants. The author suggests a new analysis for the habitat of the Lower Devonian galeaspids in Qujing on the basis of data provided by geologists and paleontologists in the last decade, particularly in 1991, including new collections of fossils and observations in the field.

The Lower Devonian stratigraphic sequence in the Cuifengshan area of Qujing is, in ascending order: the Xishancun, Xitun, Guijiatun and Xujiachong Formations.

In the Xishancun Formation of the Cuifengshan Group, the main elements of vertebrate fossils are the Galeaspida (Agnatha) and Yunnanolepiformes (Antiarch). The former includes *Polybranchiaspis minor, P. yulongssus, P. miandiancunensis, P. liaojiashanensis, Diandongaspis xishancunensis, Dongfangaspis qujingensis*, and *Damaspis vartus*; the latter includes *Yunnanolepis chii*, and *Qujinolepis gracilis*. Other fossils are marine bivalves: *Modimorpha yunnanensis, M. cf. brevis, Dysodonta deprati, D. laevis, D. orbita*, and *D. planidentata*: acritarchs: *Leiofusa* sp. and *Leiosphaeridia* sp.; chitinozoans: *Anyrochitina* sp. and *Angochitina* sp.; inarticulate brachiopods: lingulids; eurypterids and spores. It is interesting that our research group found a complete articulated branchiopod fossil in a same horizon together with *Polybranchiaspis liaojiaoshanensis* in 1991.

In the Xitun Formation of the Cuifengshan Group, the vertebrate fossils are very abundant Galeaspida: *Eugaleaspis changi, Nanpanaspis microculus, Laxaspis qujingensis*, and *Dongfangaspis major*. Thelodonti: the new genus and Thelodontidae gen. indet. Acanthodii: *Youngacanthus gracilis, Nostolepis* sp. and Ischnacanthidae indet. Sarcopterygii: *Youngolepis praecursor*

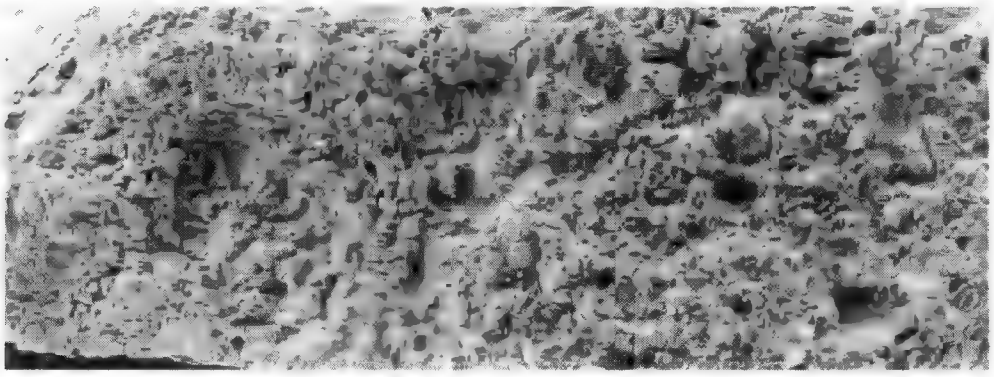


FIG. 11. — Trace fossil *Chondrites* in association with many fish scales in a bone bed of the Xitun Formation, Qujing area, Yunnan Province. IVPP V10331 (×1).

Trace fossile du genre Chondrites, *associée à de nombreuses écailles de poissons dans la Formation de Xitun, région de Qujing, Yunnan. IVPP V10331 (× 1).*

and *Diabolepis speratus*. Placodermi: *Yunnanolepis chii, Y. parvus, Qujinolepis gracilis, Phymolepis cuifengshanensis*, and *Szelepis yunnanensis*. Chondrichthyes: *Gualepis elegans, Changolepis tricuspidus, Peilepis solida*, and *Ohiolepis xitunensis*. Other fossils are marine bivalves: *Modiomorpha bicostata, M. yunnanensis, Dysodonta deprati, D. orbita*, and *D. laevis*: some complete lingulids or numerous fragments of lingulid shells in association with vertebrate microfossils were extracted from calcareous rocks by treatment with acetic or formic acids, and even many trace fossils were found (Fig. 11). I want to emphasize following facts: the marine bivalves that occur in the Xitun Formation, are often associated with vertebrate fossils, either in the same layer or in an overlying or underlying layer. Many chondrichthyan scales can be extracted both from the calcareous sandstone and the argillaceous limestone, in which some complete cranial roofs of sarcopterygians, and complete head-shield and trunk-armour of the Yunnanolepiformes were also found. The rich calcareous material indicates a transgression. The presence of chondrichthyans supports the view that the Xitun Formation was a marine deposit (WANG, 1984, 1986b) and that the vertebrates in the Xitun Formation were not of fresh water origin.

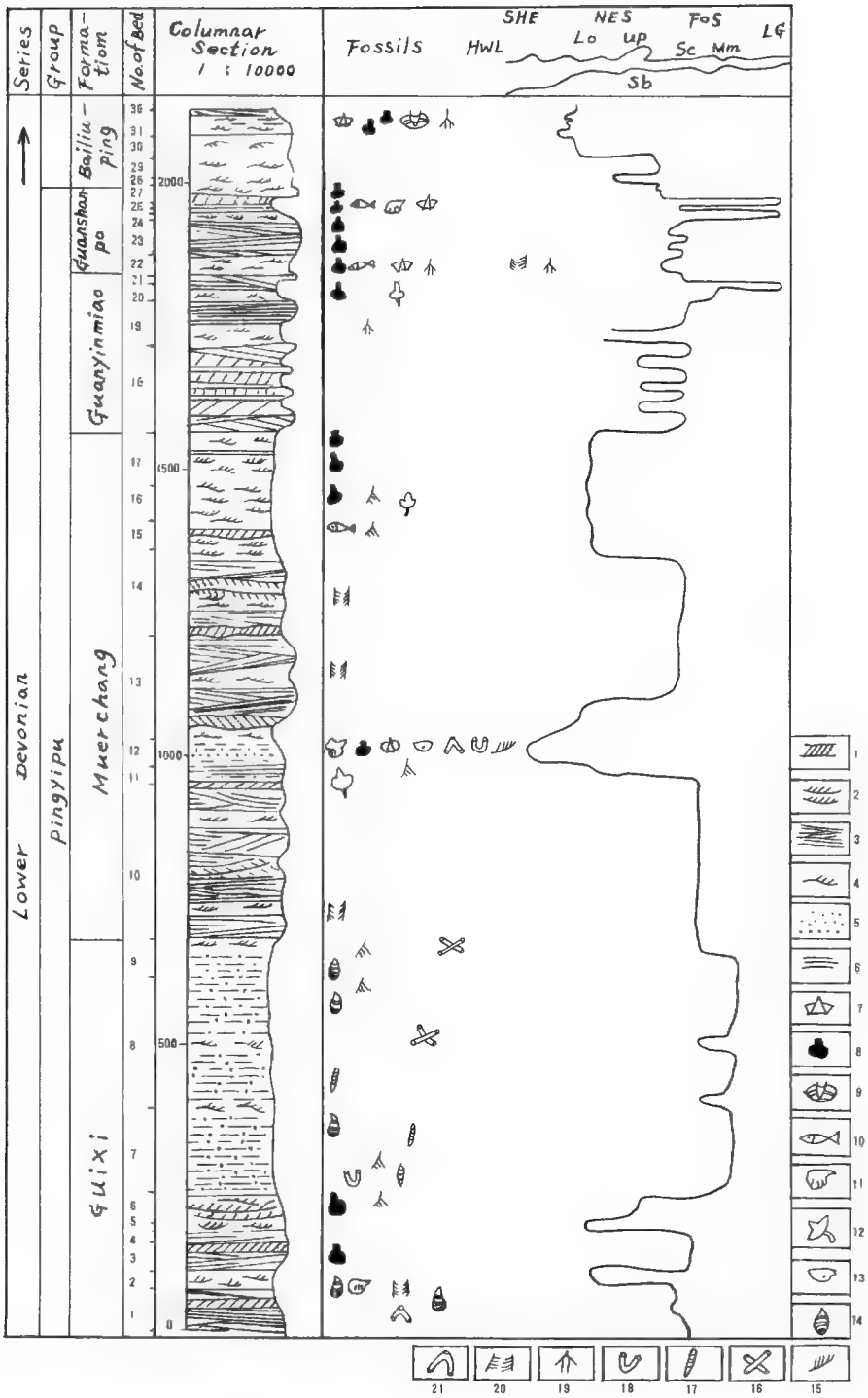
While the view of the marine condition of the Xishancun and Xitun Formations is accepted, to the contrary, the sedimentary environment of the Guijiatun and Xujiachong Formations has always been regarded as continental, primarily because the Guijiatun Formation is a red clastic rock sequence with "fresh water fish fossils" and the Xujiachong Formation has "fresh water fish fossils" and plant fossils. However, I found many layers together with vertebrates, bivalves and lingulids both in the Guijiatun and Xujiachong Formations in 1991. The same bivalves are also found in marine deposits (FANG Z.-J. pers. comm.). In the upper part of the Xujiachong Formation, there is a layer with galeaspids: *Eugaleaspis xujiachongensis*, quite similar to *E. changi* from the Xitun Formation, and a new form, associated with lingulids and marine bivalves and many plant fragments, such as *Drepanophycus spinaeformis* and *Zosterophyllum yunnanicum* (LI & CAI, 1978). Both vertebrate and invertebrate fossils are autochthonous. On the contrary, the plant fragments were clearly transported over a long distance (LIU Z.-H. pers. comm.).

Under such circumstances, there are reasons to believe that galeaspids, thelodonts, and other fishes found in the Cuifengshan Group once lived mainly in a littoral habitat. There are also other evidence in The Bac Bun Formation of northern Vietnam (corresponding to the Cuifengshan Group of East Yunnan): the layers contain a vertebrate fauna including galeaspids, and the *Howittia wangi* brachiopod fauna (TONG-DZUY & JANVIER, 1990).

Lower Devonian galeaspid-bearing strata are distributed through the Cuifengshan Group of Yunnan Province, the Pingyipu Group of Sichuan Province, the Lianhuashan and Nakaoling Formations of Guangxi Province, the Danlin, Shujiaping and Wudang Formations of Guizhou Province, and are even found in the Northeast of Vietnam.

The problem of marine versus freshwater environment can be further addressed through the analysis of the sedimentary environment in the Pingyipu Group (Lungmenshan area, Sichuan Province); the Lianhuashan and Nakaoling Formations (Liujing area, Guangxi Province), and the Danlin, Shujiaping and Wudang Formations (Guizhou Province).

A study of the sedimentary environment in the early Lower Devonian Pingyipu Group was done by TANG D.-Z., LIANG Q.-J. & DU Z.-Y. (1988). The Pingyipu Group (from the Guixi Formation up to the Guanshanpo Formation) was previously regarded as a continental deposit.


Series
Group
Formation
No of Bed
Columnar Section 1 : 10000
Fossils
SHE
NES
FoS
LG
HWL
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up
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Lower Devonian
Pingyipu
Baijiu-ping
Guanshan-po
Guanyinmiao
Muerchang
Guixi
2000
1500
1000
500
0

TANG, LIANG and DU's work both in the field and in the laboratory on the lithology, biota and sedimentary structure, resulted in an important conclusion: the sedimentary environments during the early lower Devonian Pingyipu Group are, respectively, the fore littoral zone (foreshore), near-littoral zone (nearshore), and shallow-water shelf (shelf) with clear beach characters from the southwest to the northeast (Fig. 12). The Group consists of terrestrial clastic rock, mainly light grey, medial and fine-grained quartz sandstone, with some fine-grained quartz greywacke, siltstone and mudstone, and a few grey, silty mudstones. Sedimentary structures are well preserved in this set of strata, and cross-bedding is very clear. Many trace fossil facies are also well preserved, such as *Skolithos* facies, *Cruziana* facies and *Zoophycus* facies. Fossils include brachiopods: *Howellella* sp., *Serophochonetes pingyipuensis*, *S. convexa*, *Homaffia* cf. *wangi*, and lingulids; ostracods: *Guangxinia beichuanensis*, *Beyrichia guixinensis*, and *Birdsallella sichuanensis*; bivalves, spores, chitinozoans, echinoderms, some fragments of plants and vertebrate fossil galeaspids: *Dongfangaspis major*, *Sanqiaspis sichuanensis*, *S. rostrata*, *Sinoszechuanensis yunmenpuensis*, and *Lungmenshanaspis kiangyouensis* can be found in the middle and upper parts of the Pingyipu Group in the Yanmenpao area of Jiangyou District. Therefore, the author believes that the galeaspids in the Early Devonian Pingyipu Group lived in nearshore, foreshore, and shelf manine environments.

The Liujing Devonian section in Hengxian District, Guangxi Province, is one of the most famous Devonian sections in South China. The sedimentary environments were from the front margin of the platform, then open platform to tidal flat, on a limited platform. The sediments are mainly various carbonates with few terrigenous clastic constituents (KUANG *et al.*, 1989, Fig. 3, and also see Fig. 13).

The early Lower Devonian Lianhuashan Formation and the lower part of the Nakaoling Formation were previously regarded as continental deposits by virtue of purple-red and greyish green clastic rocks and fresh water fish fossils. New works of WU Y. *et al.* (1987) and KUANG G.-D. *et al.* (1989) both in the field and in laboratory on the lithology, biota, sedimentary structure, sedimentary facies, and palaeoecology, provided a new conclusion: the sedimentary environment of the Lianhuashan Formation was littoral, with shallow, low energy, slightly-moving water in a basin which was locally closed. It changed from littoral to neritic in the early Nakaolian period (KUANG *et al.*, 1989, Fig. 19, and also see Fig. 14).

FIG.12. — Interpretation of sedimentary environment in the early Lower Devonian of Lungmenshan area, Sichuan Province, (slightly modified from TANG *et al.*, 1988, Fig. 31). FOS, foreshore; HWL, high water mark; LG, lagoon, Lo, lower part; Mm, mud mound; NES, nearshore, Sb, sand bar; Sc, sand crest, SHE, shelf; Up, upper part. 1, macrocross-stratification, 2, rough cross-stratification; 3, cross-bedding; 4, minor sand laminate bedding; 5, orthograin sequence bedding; 6, horizontal bedding; 7, articulate brachiopod; 8, chitinozoa; 9, trilobites; 10, fishes (Agnatha and fishes); 11, bivalves, 12, plants; 13, ostracods; 14, lingulids; 15, *Phycodes*; 16, *Planolites*; 17, *Skolithos*; 18, *Arenicolites*; 19, *Chondrites*; 20, *Cruziana*; 21, *Thalassinoides*.

Interprétation de l'environnement sédimentaire dans le Dévonien inférieur basal de la région de Lungmenshan, province de Sichuan, (d'après TANG et al., 1988, fig. 31, légèrement modifié). FOS, marge ; HWL, marque des hautes eaux ; LG, lagune ; Lo, partie inférieure ; Mm, monticule de vase ; NES, proche rivage ; Sb, barre sableuse ; Sc, crête de sable ; SHE, plateau ; Up, partie supérieure. 1, stratification à grands entrecroisements ; 2, stratification entrecroisée grossière ; 3, stratification entrecroisée fine ; 4, stratification de sable fin ; 5, séquence stratifiée granoclassée ; 6, stratification horizontale ; 7, Brachiopodes articulés ; 8, Chitinozoaires ; 9, Trilobites ; 10, poissons (Agnathes et poissons) ; 11, Bivalves ; 12, Plantes ; 13, Ostracodes ; 14, Lingulides ; 15, Phycodes *; 16,* Planolites *; 17,* Skolithos *; 18,* Arenicolites *; 19,* Chondrites *; 20,* Cruziana *; 21,* Thalassinoides.

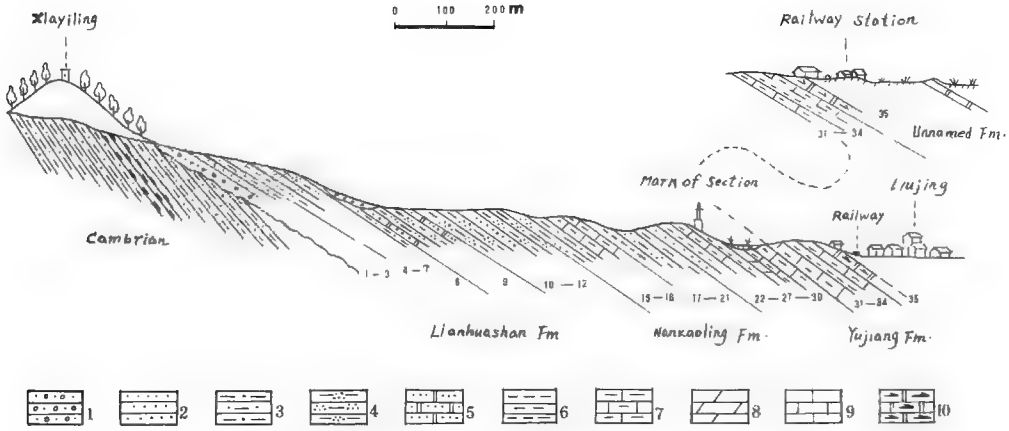

FIG. 13. — Stratigraphic section of Lower Devonian in the Liujing area, Guangxi Province, (slightly modified from KUANG *et al.*, 1989, Fig. 3). 1, conglomerate; 2, sandstone; 3, pelitic sandstone; 4, pelitic siltstone; 5, silt dolomite; 6, mudstone; 7, argillaceous limestone; 8, marl; 9, limestone; 10, siliceous dolomite.

Coupe stratigraphique du Dévonien inférieur dans la région de Liujing, province de Guangxi, (d'après KUANG et al., *1989, fig. 3, légèrement modifié). 1, conglomerat ; 2, grès ; 3, grès pélitique ; 4, silt pélitique ; 5, silt dolomitique ; 6, argilite ; 7, calcaire argileux ; 8, marne ; 9, calcaire ; 10, dolomie siliceuse.*

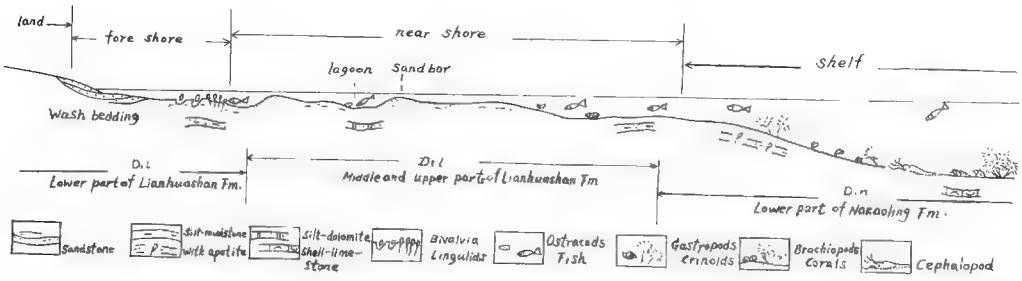

FIG. 14. — Sketch showing the sedimentary facies of the Lianhuashan-Nakaoling stages in the Liujing area, Guangxi Province, (slightly modified from KUANG *et al.*, 1989, Fig. 19).

Schéma montrant les faciès sédimentaires des étages Lianhuashanien-Nakaolingien dans la région de Liujing, Guangxi Province, (d'après KUANG et al., *1989, fig. 19, légèrement modifié).*

In the Lianhuashan Formation of Liujing area there are *Yunnanolepis* sp. and *Qujinolepis* sp. In the lowermost part of Nakaoling Formation there are the galeaspids *Asiaspis expansa, Antiquisagittaspis cornuta*, and the arthrodiran *Szelepis* sp.; and in the middle and upper parts of the Nakaoling Formation there are fishes such as acanthodians: *Gomphonchus liujingensis, Machaeracanthus? bohemicus*, and a sarcopterygian, *Onychodus* sp. (WANG, 1992).

The transgression sediments from littoral facies to neritic organic bank facies took place during the Yujiang period. The substrate was mainly a soft, sandy, and limy mud on a gentle slope (KUANG *et al.*, 1989, Fig. 22, and also see Fig. 15).

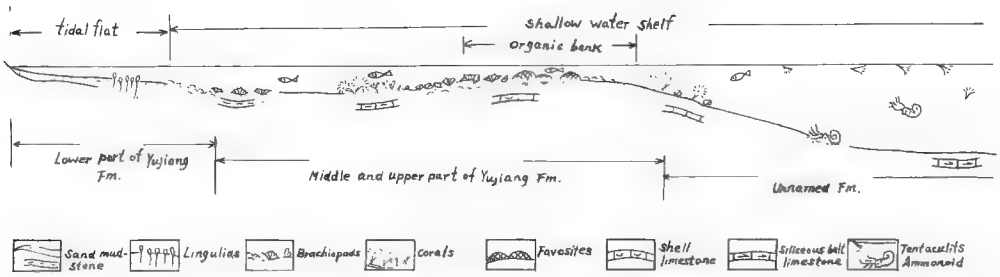

FIG. 15. — Sketch showing the sedimentary facies in the Yujiang Formation and the unnamed formation of late Early Devonian age in the Liujing area, Guangxi Province, (slightly modified from KUANG *et al.*, 1989, Fig. 22).

Schéma montrant les faciès sédimentaires dans la Formation de Yujiang et dans la formation non nommée, d'âge dévonien inférieur basal, dans la région de Liujing, province de Guangxi (d'après KUANG et al., *1989, fig. 22, légèrement modifié).*

Many microremains of vertebrate fossils have been described from the Yujiang Formation of the Liujing area, including thelodonts: *Turinia* sp., Nikoliviidae gen. indet.; acanthodians: *Cheiracanthoides comptus, Gomphonchus liujingensis*; sarcopterygians: *Onychodus* sp.; and chondrichthyans: *Ohiolepis newberryi, Wuxuanichthys wangi, Gualepis* sp., and *Hercynolepis* sp. (WANG, 1992).

The sedimentary environment of the Lower Devonian Danlin and Shujiaping Formations of Guizhou Province are respectively littoral or epicontinental littoral to neritic, judging from chitinozoans, spores and saline or brachish water algae in the Danlin Formation and by brachiopods such as *Euryspirifer paradoxus shujiapingensis, Otospirifer daleensis* in the Shujiaping Formation (HOU *et al.*, 1988).

The galeaspid *Duyunolepis paoyangensis* occurs in the lowermost part of the Shujiaping Formation of Paoyang District, *Paraduyunaspis hezhangensis* in the uppermost part of the Danlin Formation of Hezhang District, and *Neoduyunaspis minuta* in the middle part of the Wudang Formation of Wudang District, Guizhou Province. The Wudang Formation corresponds to the middle and upper parts of the Danlin Formation and the lower part of the Shujiaping Formation (Fig. 16).

With respect to the lower Devonian galeaspid-bearing sedimentary environments in Yunnan, Sichuan, Guangxi and Guizhou Provinces, the above data lead to the conclusion that the galeaspids lived completely in marine (littoral to neritic) environments. They were possibly euryhaline agnathans but no fresh water ones.

The problem can be also resolved from the analysis of the Silurian galeaspid environments and Silurian and Lower Devonian red clastic rocks.

Silurian galeaspids have been mainly reported from the region of the middle and lower reaches of the Yangtze River. The oldest reported galeaspid-bearing stratum is the Rongxi Formation of Dayong District, Hunan Province, with the galeaspid *Dayongaspis hunanensis*. The formation is mainly composed of red, yellow or greyish green silty mudstone and contains brachiopods: *Nalivkinia, Nucleospira, Isorthis, Striispirifer*; trilobites: *Logiashania*; graptolites: *Hunanodendrum*; and crinoids: *Pisocrinus* (Fig. 17).

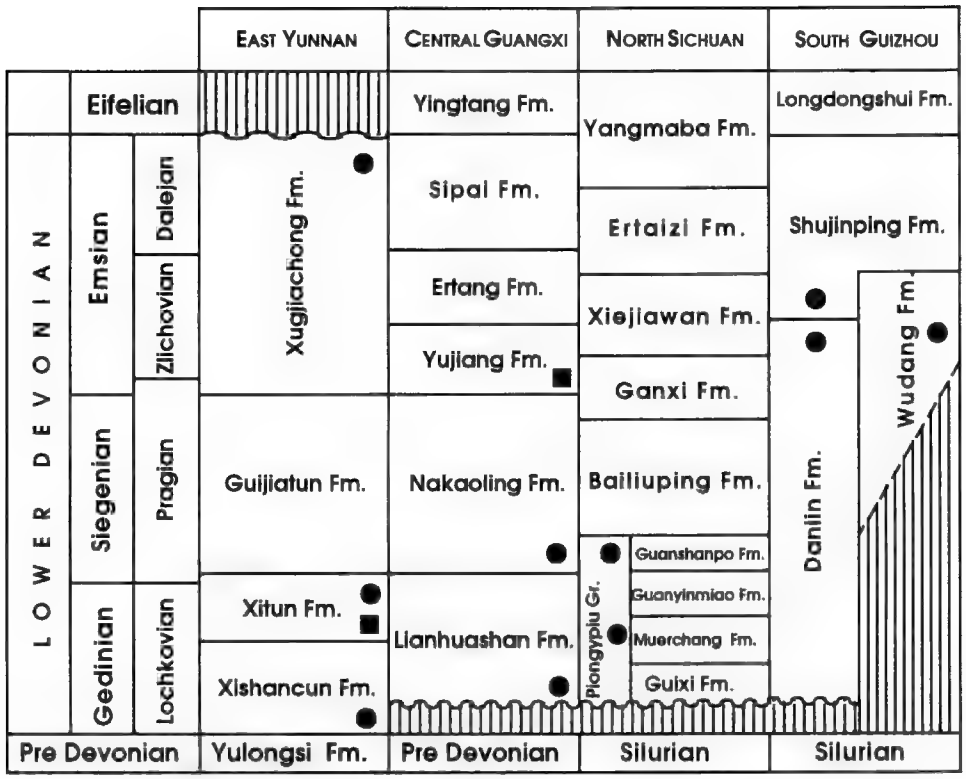

FIG. 16. — Classical correlation of the galeaspid and thelodont bearing strata of the Lower Devonian in China. Round marks, galeaspids; square marks, thelodonts.

Tableau des corrélations classiques entres les niveaux à Galéaspides et à Thélodontes dans le Dévonien inférieur de Chine. Marques rondes, Galéaspides ; carrées, Thélodontes.

The overlying upper Xiushan Formation contains a diverse shell fauna of mostly brachiopods: *Salopinella*, *Xinanospirifer*, *Nalivkina*, *Atrypoidea*, and *Atrypopsis*; trilobites: *Coronaspis*, *Coronocephalus rex*, *Kailia*, and *Rongxiella*; nautiloids: *Sichuanoceras*; graptolites: *Stomatograptus sinensis*; conodonts: *Pterospathodus celloni*; and chitinozoans: *Angochitina longicollis* (RONG & CHEN, 1990). The Xiushan fauna has been widely encountered in the Late Llandovery Goudingshan Formation of Wuhan city, Hubei Province with the galeaspid *Hanyangaspis guodingshanensis*, and in the Fentou Formation of Chaoxian District, Anhui Province, with the galeaspid *Latirostraspis chaohuensis*.

The so-called Upper Red Beds of the Silurian contain the galeaspid-bearing formations: Huixingshao, Xikeng, and Maoshan formations, all overlying the Xiushan Formation. The

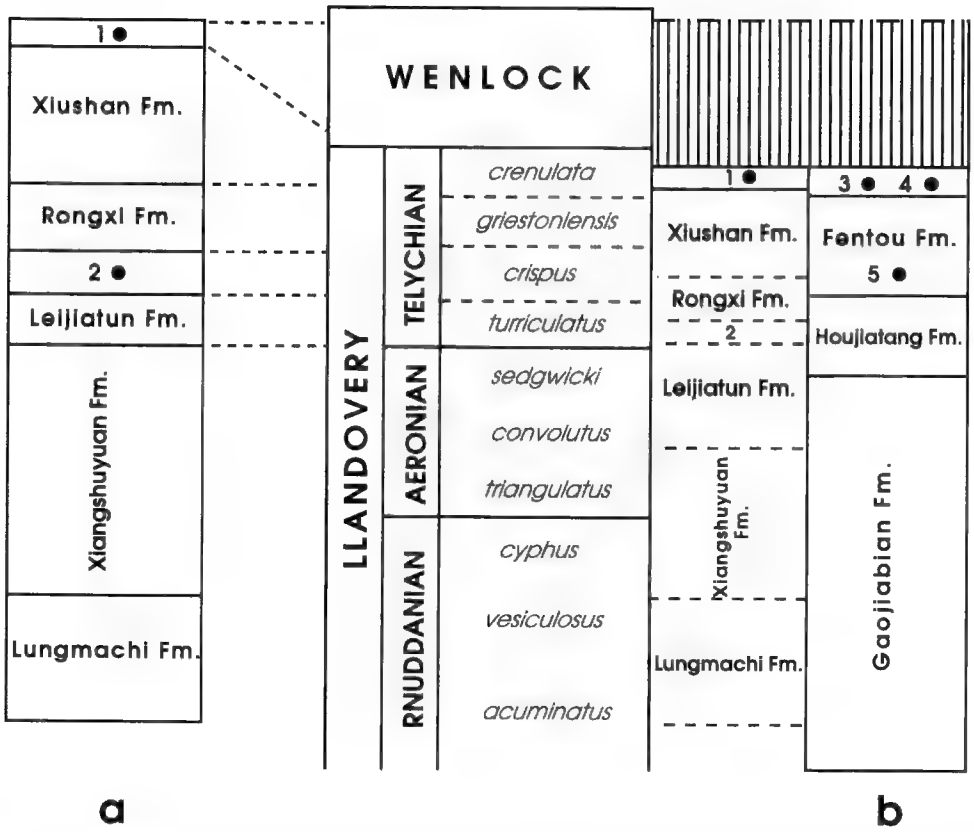

FIG. 17. — Different opinions on the age of the Lower Silurian galeaspid and thelodont-bearing strata in China. A, after N.-Z. MU *et al.*,, 1982; B, by RONG & CHEN, 1990. 1, Huixingshao Formation; 2, Majiachong Formation; 3, Maoshan Formation; 4, Xikeng Formation; 5, Guodingshan Formation. Round marks, galeaspids; square marks, thelodonts.

Différentes opinions sur l'âge des niveaux à Galéaspides et Thélodontes dans le Silurien inférieur de Chine. A, selon N.-Z. MU et al., *1982 ; B, selon RONG & CHEN, 1990. 1, Formation de Huixingshao ; 2, Formation de Majiachong ; 3, Formation de Maoshan ; 4, Formation de Xikeng ; 5, Formation de Guodingshan. Marques rondes, Galéaspides ; carrés, Thélodontes.*

Huixingshao Formation of Xiushan District of Sichuan Province includes the galeaspid *Eugaleaspis xiushanensis* (LIU, 1983). The Xikeng Formation of Xiushui District, Jiangxi Province, includes galeaspids: *Sinogaleaspis shankonensis*, *S. xikengensis*, *Xiushuiaspis jiangxiensis*, and *X. ganbeiensis* (P'AN & DINELEY, 1988). The Maoshan Formation of Changxing District, Zhejiang Province includes galeaspids: *Sinogaleaspis zhejiangensis* (P'AN & WANG, 1981), *Changxingaspis gui*, and *Meishanaspis lehmani* (WANG, 1991). Other fossils in the Upper Red Beds are gastropods: *Discodichilus* sp., bivalves: *Modiolopsis* sp. and microfossils: *Leiosphaerida eisenachia*, *L. laeviguta*, *L. pilorum*, *L. citrinus*, *Trachysphaeridium* sp., *Lophosphaeridium* cf. *parverarus*, and *Macrohystridium nainacanthus*. In addition, the Wujiahe Formation of Ziyang District,

Shaanxi Province includes Galeaspida gen. et sp. indet. in conjunction with graptolites in the same horizon. It should be evident from the above data that the Silurian galeaspids lived in a marine environment.

It is interesting that agnathan (galeaspid and thelodont) bearing strata are mostly purple, red clastic rocks both in Silurian and Lower Devonian; such as the so-called Lower Red Beds, the Lower Silurian marine Rongxi Formation; the so-called Upper Red Beds, the Lower Silurian marine Xikeng, Maoshan and Huixingshao formations; the Upper Silurian Guandi Formation; the Lower Devonian Lianhuashan Formation; the Guijiatun Formation and the Wudang Formation. The data from the Lianhuashan Formation can help us to understand the marine clastic rock sequences. There are some vertical U-shaped dwelling trails, many lingulids in their living condition with muscle scars, as well as some *Skolithos* in the lower part of the Lianhuashan Formation, which indicate typical tidal flat, sandy to muddy sediments.

The features of the sediments in the middle and upper parts of the Lianhuashan Formation are fine-grained clasts with much mud, mainly purple-red in colour, small to medium-sized wave-generated cross beddings, and oblique cross beddings in the sandstone or siltstone. The amount of B-elements exceeds 120 ppm. In addition, there are some fossils, such as ostracods, bivalves, brachiopods and gastropods, and particularly trace fossils, such as *Cruziana*, *Chondrites*, *Zoophycus*, *Skolithos*, *Phycodes*, *Planolites*, *Arenicolites*, and *Thalassinoides*. It is clear that the sedimentary environment in the middle and upper parts of the Lianhuashan Formation indicates a sublittoral zone condition with shallow, lower energy, slightly moving water bodies, in a locally closed area. The purple colour of the strata is to be expected in the presence of iron (Fe, 3-valences), and even biotite and illite in weathering conditions (KUANG *et al.*, 1989).

CONCLUSIONS

1) The Chinese fossil jawless craniates contain the endemic Galeaspida and cosmopolitan as well as endemic Thelodonti. No fossil of both the Osteostraci and Heterostraci has been discovered in China. Galeaspids are found mainly in the Early Silurian and Early Devonian of South China, and thelodonts in the Late Ludlovian to Givetian of southwestern China.

2) The data from the external morphological characters of the Galeaspida are fairly complete. Here a important character is defined: a pair of lateral or medial dorsal fenestrae in the dorsal shield in certain forms. Many internal anatomical characters are extremely well preserved, particularly the structure in front of the telencephalic portion in *Changxingaspis gui* WANG, 1991, such as long, paired terminal and olfactory nerve canals, a pair of separate nasal sacs lacking an ossified floor, and joining outwards and forwards with a large exonasal opening in the dorsal shield.

3) The pattern and structure of the sensory line system in the dorsal shield of the Galeaspida differs greatly from that of the Osteostraci or the Heterostraci. The sensory line system in the dorsal shield of the Galeaspida is well developed both in the form of canals in the bony exoskeleton and in the form of superficial grooves.

4) The feature of a pair of lateral or medial dorsal fenestrae is a synapomorphy of the fenestrate galespids, and the order Macrothyraspidida, which display this feature, are a mono-

phyletic group. The orders Eugaleaspidiformes and Huananaspidiformes, previously regarded as two monophyletic groups within the Galeaspida, are confronted to a serious challenge.

5) Silurian and Devonian jawless craniates (Galeaspida and Thelodonti) in China had a littoral or neritic habitat, judging from the data on the associated marine fossils and from the analysis of the fish-bearing sedimentary facies. They were euryhaline agnathans, not fresh water ones.

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Placoderm diversity and evolution

by Robert K. CARR

Abstract. — Stratigraphic ranges for 720 placoderm taxa are presented and diversity patterns are characterized for six monophyletic placoderm orders as well as for other Devonian and Mississippian gnathostomes. Analysis at the level of substage is critical for the recognition of placoderm subclade diversity patterns. The current temporal and taxonomic resolution of individual placoderm taxa is sufficient to provide a clear picture of diversity independent of the level of resolution selected for screening data. Analysis of all available data provides the best picture of placoderm diversity. Current hypotheses of arthrodiran competitive displacement represent global patterns and require careful consideration of patterns of phylogeny, geographic distribution, and ecological sympatry. These considerations provide alternative interpretations of timing of events and influence the analyses of alternative hypotheses of biological interactions (competitive or opportunistic replacements or chance). Pachyosteomorph arthrodiran diversity may be correlated with morphological evolution related to adaptations associated with feeding and locomotion. Gnathostome diversity suggests that Devonian extinction episodes are not ubiquitous events with clades showing different responses to three putative Upper Devonian extinctions (Givetian-Frasnian, Frasnian-Famennian, and Famennian-Tournaisian). The Frasnian-Famennian extinction event had a significant effect on placoderms. This event may have reduced the numbers of placoderms sufficiently to provide a "window of opportunity" for the early radiation of actinopterygians and chondrichthyans. During the Famennian there is evidence for predator-prey relationships and potential competition for resources among surviving placoderms and other gnathostomes. These biological interactions are coincident with an inverse relationship between placoderm diversity patterns and those for actinopterygians and chondrichthyans. This coincidence suggests that the extinction of placoderms may be attributed to competitive displacement although opportunistic replacement following the putative Famennian-Tournaisian extinction event remains as an alternative explanation.

Keywords. — Placoderms, evolution, diversity, monophyletic orders, Devonian extinctions.

Diversité et évolution des Placodermes

Résumé. — Les répartitions stratigraphiques de 720 taxons de Placodermes sont présentées et leur diversité est définie pour six ordres de Placodermes ainsi que pour d'autres Gnathostomes dévoniens et mississippiens. L'analyse au niveau du sous-étage est cruciale pour la connaissance de la structure de la diversité des sous-clades de Placodermes. L'actuel degré de résolution temporelle et taxonomique de chaque taxon de Placoderme est suffisant pour donner une image nette de leur diversité, indépendamment du niveau de résolution choisi pour l'examen des donnees. L'analyse de toutes les données disponibles fournit la meilleure image de la diversité des Placodermes. Les hypothèses actuelles sur les déplacements liés à la compétition chez les arthrodires produisent des structures de répartition globales et demandent une attention particulière à l'egard de la phylogenie, de la distribution géographique et de la sympatrie. Ces considérations conduisent à des interprétations alternatives des évènements chronologiques et influencent l'analyse des hypothèses possibles sur les interactions biologiques (remplacement compétitif ou opportuniste, ou hasard). La diversité des arthrodires pachyostéomorphes peut être corrélée avec une évolution morphologique liée à des adaptations du régime alimentaire ou de la locomotion. La diversité des Gnathostomes suggère que les épisodes d'extinction au Dévonien ne sont pas des évènements ubiquistes, car des clades montrent différentes réponses aux extinctions présumées du Dévonien supérieur (Givétien-Frasnien, Frasnien-Famennien et Famennien-Tournaisien). L'extinction du Frasnien-Famennien a eu un effet significatif sur les Placodermes. Cet évènement peut avoir réduit leur nombre suffisamment pour offrir une chance à la première radiation des Actiniptérygiens et Chondrichthyens. Pendant le Famennien, on a la preuve d'une relation prédateur-proie et d'une compétition potentielle pour les resources entre les Placodermes et les Gnathostomes survivants. Ces interactions biologiques coïncident avec une relation inverse entre la diversité des Placodermes et celle des Actinoptérygiens et Chondrichthyens. Cette coïncidence suggère que l'extinction des

Placodermes peut être attribuée à une compétition, bien que des remplacement opportunistes à la suite de l'extinction présumée du Famennien-Tournaisien restent une explication alternative.

Mots-clés. — Placodermes, évolution, diversité, groupes monophylétiques, extinctions dévoniennes.

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Introduction

Placoderms, known from the latest Silurian to the earliest Mississippian, offer an excellent model for the analysis of evolutionary patterns and mechanisms at a time early in gnathostome history. Not only do placoderms represent a morphologically and ecologically diverse group, the most speciose gnathostome clade present from the earliest Devonian until the latest Frasnian, but their extinction was associated with several putative global extinctions and the radiation of other gnathostomes. Although placoderms have been studied for many years, a number of fundamental questions remains. Early attempts to understand the biology of placoderms were hindered by numerous misconceptions about their evolutionary history. This has required reanalysis of anatomy, taxonomy and systematics (e.g. Miles, 1969; Miles & Young, 1977; Miles & Dennis, 1979; Goujet, 1984a, b; Lelièvre *et al.*, 1981; Young, 1981; Forey & Gardiner, 1986; Ivanov, 1988; Lelièvre, 1988; Long, 1990a; Vézina, 1990; Gardiner, 1990; Carr, 1991). From this new foundation, a better understanding of placoderms is emerging along with important information concerning other vertebrates. This study provides a current summary of placoderm species, along with their stratigraphic ranges, and an analysis of placoderm diversity patterns for species- and genus-levels (number of taxa per stage or substage).

A number of hypotheses have been put forth concerning the nature and number of global extinctions during the Devonian (House, 1985; Sepkoski, 1986; McMillan *et al.*, 1988). Gnathostome diversity patterns are evaluated in light of these hypotheses and hypotheses of biological interactions among gnathostomes. Ecological replacement (opportunistic replacement), competitive displacement, and chance have been proposed to explain patterns of temporal replacement of one group or clade by another. Miles (1969) and Gardiner (1990) provided a hypothesis for the succession of competitively superior levels among arthrodiran placoderms. Their assumptions are subjectively evaluated, based on current phylogenetic and diversity patterns. Additionally, other comparisons among placoderm clades are evaluated along with necessary precautions related to assumptions of biological interactions. A number of morphological changes have been documented among brachythoracid arthrodires with pachyosteomorph arthrodires showing a significant diversity increase. Evaluation of adaptive aspects of these changes suggest a correlation between pachyosteomorph diversity and improvements in feeding and locomotion.

Abbreviations

Aup	autopalatine ossification of the palatoquadrate, *ossification autopalatine du palatocarré*;
cr.art	articular crest of the scapulocoracoid, *crête articulaire du scapulocoracoïde*;
Hm	hyomandibula, *hyomandibulaire* ;

IG	inferognathal plate, *inférognathale*;
MD	median dorsal plate, *plaque médiane dorsale*;
Mk	Meckel's cartilage, *cartilage de Meckel*;
PVL	posterior ventrolateral plate, *plaque ventrolatérale postérieure*;
Qu	quadrate ossification of the palatoquadrate, *ossification carrée du palatocarré*;
SO	suborbital plate, *plaque suborbitaire*;
scler	sclerotic plate, *anneaux sclérotiques*.

MATERIAL AND METHODS

Appendix I provides a species level compilation of stratigraphic ranges for all placoderms (DENISON, 1978; placoderm references from the Zoological Record, 1975-1991). It includes taxonomically and temporally ambiguous taxa (e.g. indeterminate material, unresolved synonyms, species based on fragmentary material, *incertae sedis*). Indeterminate taxa are included whenever they provide temporal range information or represent forms from distinct geographic regions. Temporal resolution for taxa ranges from indeterminate to substage (50 species without stratigraphic resolution to series are recorded in Appendix I, but are not included in diversity analyses). A range through method is used for taxa with poor stratigraphic resolution (e.g. a Frasnian occurrence is recorded as a Lower to Upper Frasnian presence at the substage level). Also included is unpublished data from research in progress (indicated in Appendix I as "n. sp.", CARR & HLAVIN, in press, *Dunkleosteus* n. sp. 1, *D.* n. sp. 2; CARR, MS. *Stenosteus* n. sp. -pers. comm.- LELIÈVRE, *Maideria falipoui*, this volume). A total of 720 taxa are recorded with diversity patterns (number of taxa per unit of time) analyzed at different levels of temporal and taxonomic resolution (among the 720 taxa there are 267 recognized genera and 591 recognized species. Thirty-three forms are indeterminate to a generic level with an additional 41 species having questionable assignments to generic level. Seventy-five taxa assigned to a genus lack assignment of a species name; recorded as "sp.". Eight taxa represent species provisionally assignable to other recognized species; recorded as "cf.". One conferrable genus is recorded. Seven questionable species assignments are recorded with one specific variety noted.). Extinction levels for the Frasnian-Famennian boundary are recorded for both species- and genus-levels and at stage- and substage-levels of analysis (table 1).

It is important to consider the level and units of analysis to be used in the study of diversity. Placoderm data suggest substage-level analyses are necessary to clearly evaluate subclade patterns. The resolution of the individual data is less critical; however, this may be due solely to the relatively low level of indeterminate taxa (4.6% indeterminate to genus and 5.7% with questionable generic assignments) and taxa with poor stratigraphic resolution (6.8% not resolved to series (epoch) and 11.9% resolved to series). Stage names follow those of DENISON (1978) which are used in his compendium. No effort has been made to convert DENISON's Early Devonian stage names (Gedinnian and Siegenian) to current formal names (Lochkovian and Pragian) since exact stratigraphic data is not available for an accurate conversion (refer to HARLAND *et al.*, 1989, for a discussion of the relationship between formal names and those used by DENISON, 1978). Stage names for the last appearance data taken from SEPKOSKI (1992) follow those of HARLAND *et al.* (1989).

From these data, the diversity patterns for a number of monophyletic placoderm groups are described and compared. Additionally, the generic diversity for all remaining Devonian and Early Mississippian gnathostomes is evaluated to document patterns of change during this critical time in vertebrate history. Data for chondrichthyans (ZANGERL, 1981; CARROLL, 1988), and acanthodians (DENISON, 1979) are recorded at stage level; however, osteichthyan data (taxonomy and range data from CARROLL, 1988) are recorded using series. MILES' (1969; see also GARDINER, 1990) characterization of arthrodiran evolution as a succession of competitively superior grades is specifically considered by subjectively comparing his and current estimates of arthrodiran clades against predicted patterns for competitive and opportunistic replacements. The radiation of pachyosteomorph, or more specifically aspinothoracid, arthrodires in the Late Devonian is evaluated. Morphological changes within this clade are compared through analogy with extant fishes and mechanical aspects of these changes are evaluated in terms of biological roles and mechanical effectiveness.

The specimen number prefix CMNH denotes the Cleveland Museum of Natural History. The suffix "id" when used to form taxonomic adjectives does not refer to family-level Linnean classification and is used as a convenience for discussing informal taxonomic units. Abbreviations for stage names used in figures and Appendix I follow that of HARLAND *et al.* (1989).

RESULTS

PATTERNS OF DIVERSITY FOR PLACODERMS

Placoderm global diversity rose at a nearly steady rate from the Silurian to the Frasnian-Famennian boundary reaching both generic and specific peaks within the Frasnian (Fig. 1; see also GARDINER, 1990). At the Frasnian-Famennian boundary current data suggest an overall placoderm species extinction of 48-51% and a generic extinction of 52-53% (table 1).

The genus- and species-level diversity patterns for placoderms are equivalent for both substage and stage-level analyses of all available data, only minor fluctuations are noted at substage levels (Fig. 1). Figure 2 demonstrates similar generic patterns for:

1) stage-level analysis of all available data;

2) data with a temporal resolution to stage level or finer;

3) taxonomically resolved data (indeterminate forms and doubtful generic assignments are excluded);

4) and data resolved both temporally and taxonomically.

The orders Rhenanida (*sensu stricto, i.e.*, excluding palaeacanthaspids) and Petalichthyida (Figs. 3A, B, 4-5) showed low specific diversity from their first appearance in the Gedinnian to their final appearance in the Upper Frasnian (Upper Devonian records are represented by single species). Both orders were marine and have been characterized as being dorsoventrally compressed (DENISON, 1978). This characterization is seen in *Gemuendina stuertzi* (a rhenanid, Fig. 3B) with its dorsally placed orbits and enlarged ray-like pectoral fins; however, little is known concerning the body form among petalichthyids. *Lunaspis broilii* (Fig. 3A), one of the better known petalichthyids from the Hunsrückschiefer of Germany, has been secondarily com-

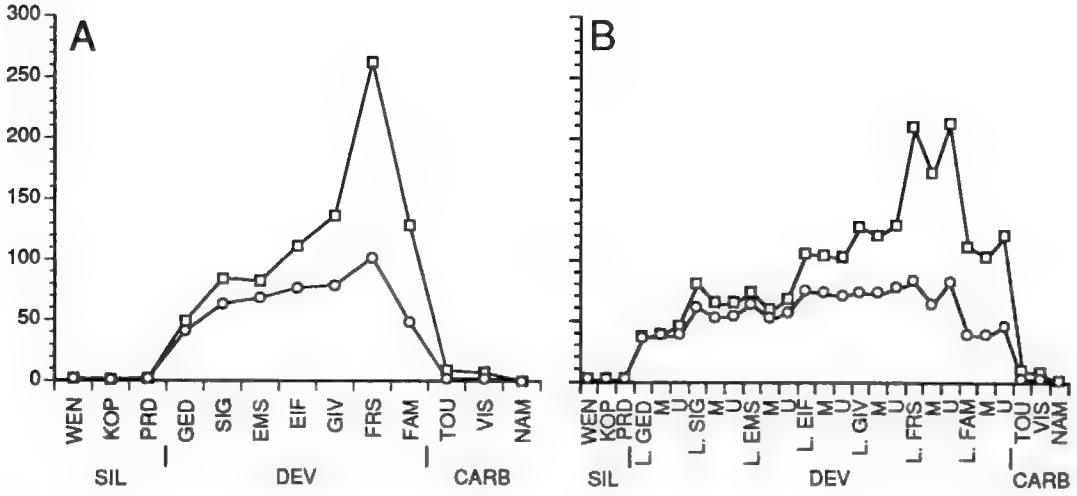


FIG. 1. — Placoderm diversity utilizing all available data demonstrating equivalent patterns among differing levels of analysis. A, stage-level analysis of specific (squares) and generic (circles) diversity. B, substage-level analysis.

Analyse de la diversité des Placodermes utilisant les données disponibles et montrant les modèles équivalents à différents niveaux. A, données sur les espèces (carré) et sur les genres (cercle) en fonction des étages géologiques. B, mêmes données en fonction des sous-étages.

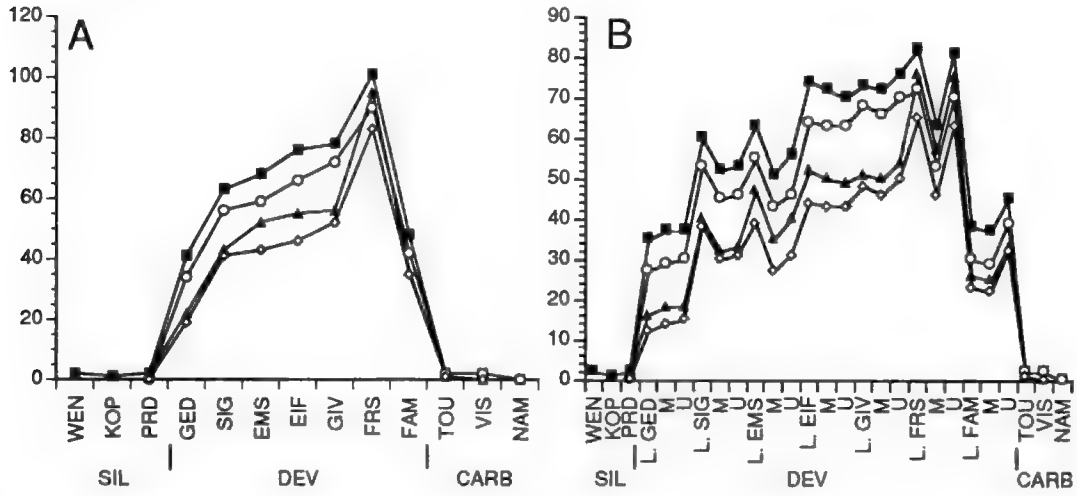


FIG. 2. — An analysis using alternative screening criteria for placoderm data. Results of the analysis demonstrate equivalent diversity patterns for each screening criterion. Placoderm generic diversity (squares) utilizing all data; data taxonomically resolved to genus with indeterminate forms omitted (circles); temporally resolved taxa to stage level or finer (triangles); and both taxonomically and temporally resolved data (diamonds). A, stage-level analysis. B, substage-level analysis.

Analyse utilisant les criteres alternatifs sur les données des Placodermes. Les résultats de cette analyse mettent en évidence des modèles de diversité équivalents pour chaque critère. Diversité générique des Placodermes (carrés) ; donnée taxonomiquement résolue au niveau du genre avec les formes indéterminées omises (cercles) ; taxons résolus au niveau de l'étage géologique ou plus (triangles) ; données résolues taxonomiquement et temporellement (losanges). A, analyse par étage géologique. B, analyse par sous-étage géologique.

pressed during preservation. Little information is obtainable from other petalichthyids, concerning body form, other than the partial shift of the orbits onto the head shield. Rhenanids disappeared from the North American craton during the Frasnian-Famennian extinction episode (Upper Frasnian last appearance) well after the Middle-Upper Devonian facies transition from shallow water carbonates to anoxic clastic deposits. Petalichthyids survived into the Famennian. However, petalichthyid and rhenanid low global diversities argue against the attachment of any particular significance to their final disappearance.

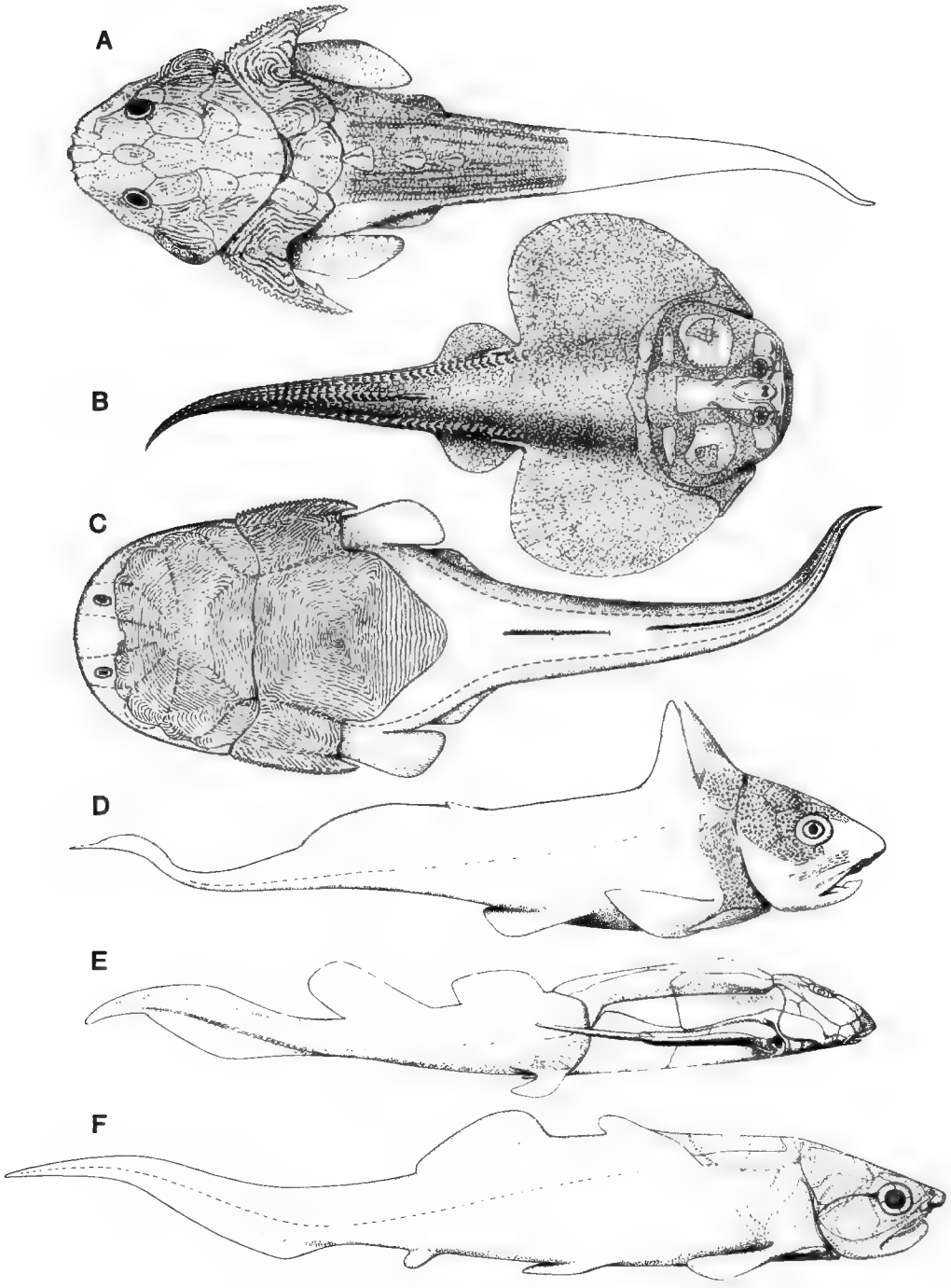
The order Phyllolepida (Figs. 3C, 4-5) was clearly present in the Frasnian and survived until the end of the Devonian. They reached their highest specific diversity after the Frasnian-Famennian extinction episode. An earlier Eifelian first appearance may be indicated if *Antarctaspis* (whose stratigraphic range is unclear, *i.e.* Middle or Upper Devonian) is considered as a member of Phyllolepida (family Antarctaspidae is considered here Arthrodira *incertae sedis*). Phyllolepida were thought to be restricted to freshwater by DENISON (1978; BENDIX-ALMGREEN, 1976), although LERICHE (1931) concurred, he noted the lateral association between Belgian marine Schistes de la Famenne and Psammites et Schistes d'Evieux which now suggests the possibility that these latter phyllolepid deposits are potentially marginal marine. Recent analyses also have called into question a non-marine interpretation for some Old Red Sandstone style sediments (see discussion below). Phyllolepids survived the Frasnian-Famennian extinction (table 1) with a specific increase, but a without generic change; however, low specific diversity limits analysis.

The order Antiarcha (Figs. 3D, 4-5) first appeared in the Silurian of China and possibly survived to the Lower Carboniferous (seven of the eight species recorded from the Carboniferous are resolved temporally to series-level, *i.e.* Lower Carboniferous, suggesting that diversity plots for antiarchs, figures 1, 2, 5, and 10, may artificially extend their range through the Visean). Diversity during the Lower Devonian remained stable with successive increases seen in the Eifelian, Givetian, and Frasnian when they finally reached their peak. Again, many species are known from Old Red Sandstone facies. Antiarch extinction across the Frasnian-Famennian boundary was between 30-58% (table 1).

The order Ptyctodontida (Figs. 3E, 4-5) first appeared in the Siegenian with their last appearance in the Famennian (*Tollodus brevispinus* is recorded from the Siegenian of the Soviet Arctic, ØRVIG, 1980b, with other genera first appearing in the Eifelian). After the Eifelian, specific diversity continued to increase until the Frasnian-Famennian extinction episode when 75-77% of ptyctodont species went extinct (table 1). Generic diversity remained level from the Eifelian through the Frasnian with a 71% decline of known genera at the Frasnian-Famennian boundary.

FIG. 3. — Representative reconstructions for members of the placoderm orders discussed in the text. A, *Lunaspis broilii*, dorsal view. A, a petalichthyid B, *Gemuendina stuertzi*, dorsal view, a rhenanid. C, *Phyllolepis orvini*, dorsal view of head and thoracic shields, a phyllolepid; D. *Ctenurella gladbachensis*, a ptyctodont, lateral view. E, *Bothriolepis canadensis*, an antiarch, lateral view. F, *Coccosteus cuspidatus*, a brachythoracid, lateral view. A-F taken from STENSIÖ, 1963.

Reconstitutions de divers taxons d'ordres de Placodermes présentés dans le texte. A, un petalichthyide. Lunaspis broilii, *vue dorsale. B, un rhénanide.* Gemundina stuerzi *en vue dorsale. C, un phyllolépide.* Phyllolepis orvini, *vue dorsale des cuirasses crânienne et thoracique. D, un ptyctodonte,* Ctenurella gladbachensis *en vue latérale. E, un antiarche,* Bothriolepis canadensis *en vue latérale. F, un brachythoracide.* Coccosteus cuspidatus *en vue latérale. Figures A-F reprises de STENSIÖ, 1963.*


A
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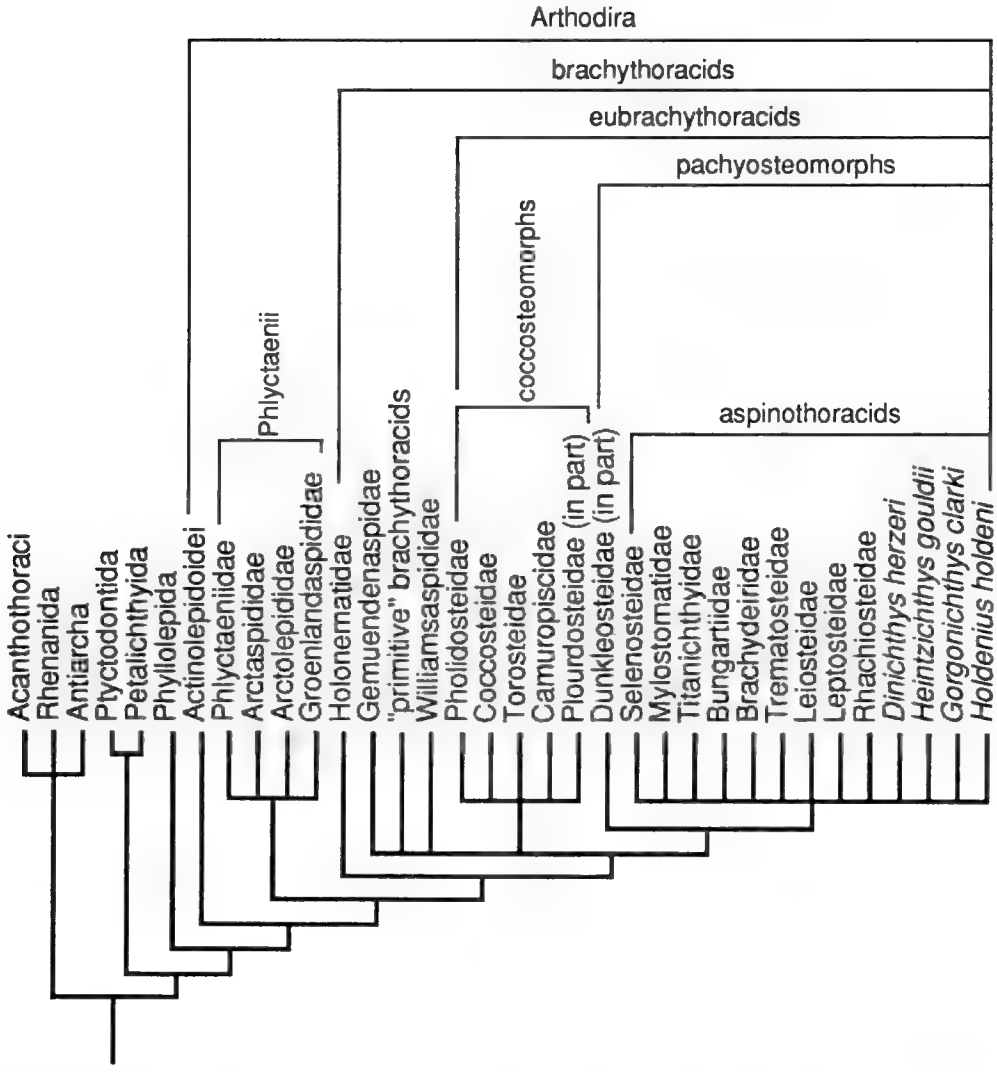

FIG. 4. — Cladogram indicating generalized phylogeny within Placodermi. Modified from GOUJET (1984b), GARDINER (1990), and CARR (1991).

Cladogramme des Placodermes modifié d'après GOUJET (1984b), GARDINER (1990), et CARR (1991).

The order Arthrodira (Figs. 3F, 4-5) has been reported from the Wenlockian (PAN & DINELEY, 1988), although, GOUJET (pers. comm.) suggests these Chinese forms are not true arthrodires. Arthrodires are known with certainty from the Ludlovian to possibly Tournaisian and showed an increase in diversity from first appearance to the Siegenian, from which point they maintained

stable levels until the Frasnian. Peak diversity was achieved in the Upper Frasnian followed by a dramatic drop at the Frasnian-Famennian boundary (57-62%, table 1). Figure 6 presents generic diversities for Actinolepidoidei, Phlyctaenii, coccosteomorph, and pachyosteomorph arthrodires based on both MILES' (1969) and current classifications (see discussion below).

PATTERNS OF DIVERSITY FOR OTHER GNATHOSTOMES

Chondrichthyans are first recorded from the Lower Silurian (NOVITSKAYA & KARATAYUTE-TALIMAA, 1986; KARATAYUTE-TALIMAA, 1992) with a significant increase in diversity at the Devonian-Mississippian boundary (Fig. 7A). Approximately 50% of this increase is accounted for by isolated teeth, denticles (dermal and mucus membrane), and other ichthyodorulites. Among chondrichthyans, the Subterbranchialia (ZANGERL, 1981) and elasmobranchs have similar patterns with elasmobranchs possessing greater numbers.

Acanthodians (Fig. 7B), with bimodal peak generic diversities in the Siegenian and Eifelian, demonstrated a relatively gradual decline throughout the Devonian and Carboniferous until their extinction in the Permian. A moderate increase in the rate of decline is noted at the Frasnian-Famennian boundary. Among the three recognized orders of acanthodians (DENISON, 1979), the climatiids and ischnacanthids appear to account for the earlier peak in diversity while climatiids and indeterminate specimens account for the latter acanthodian peak. Low diversity among these orders hinders further analysis.

Among sarcopterygians (taxonomy after CARROLL, 1988), Onychodontiformes, Holoptychoidea, and Dipnoi first appear in the Lower Devonian (CARROLL, 1988; Fig. 8). Osteolepidoidea first appear in the Middle Devonian (CARROLL, 1988) and are followed in the Frasnian by coelacanthiformes and Tetrapoda. Sarcopterygians, recorded here at an epoch level of resolution, demonstrated an increase in generic diversity from the Givetian to Frasnian. Diversity changes during the Frasnian-Famennian extinction episode cannot be evaluated due to the lack of resolution. In contrast, actinopterygians (Fig. 8B) showed little or no increase from first appearance in the Middle Devonian (CARROLL, 1988) until the Tournaisian. During the final decline of placoderms we see a similar decline in rhipidistians and dipnoans, although, not to complete extinction with the exception of onychodonts. Coelacanth diversity remained relatively stable during the Late Devonian and Early Mississippian, but again, this may reflect a lack of resolution.

DISCUSSION

DIVERSITY PATTERNS

Although the fossil record is a filtered view of "true" diversity (RAUP, 1979, notes biases due to taxonomic level, geographic distribution, taphonomy, sampling, and rock availability), this record represents the only source of information for extinct taxa like placoderms. In considering evolution and extinction, it is important to recognize that diversity patterns reflect outcomes of both physical and biological interactions. Additionally, in evaluating global diversity it is important to consider patterns of phylogeny and geographic distribution. With the above

information, one can begin to evaluate specific hypotheses of extinction effects, biological interactions, and morphological evolution.

During the Devonian there was a major radiation within gnathostomes. The water column, in which these fishes lived, was not devoid of other predators; however, the history of early vertebrates shows the origin and evolution of organisms with specializations in locomotion, feeding structures, and sensory organs, as well as central processing and coordination of sensory and motor systems (NORTHCUTT & GANS, 1983). The appearance of these new morphologies are suggestive of an adaptive radiation.

Devonian sediments potentially offer an unique and important view of early gnathostome history since they represent the largest estimated volume and geological map area for Paleozoic systems (DINELEY, 1984). The globally distributed Old Red Sandstone developed during this period and was associated with a number of tectonic events. A major facies shift occurred within the series of North American carbonate basins at the beginning of the Upper Devonian, characterized by the widespread deposition of anoxic black shales. The Upper Devonian further represents a time of complex biotic and abiotic events which include numerous orogenies putatively associated with the suturing of Pangaea (MCMILLAN *et al.*, 1988). JOHNSON (1970) noted shifts among brachiopods from earlier provincialism to cosmopolitanism associated with Upper Givetian onlap, effectively lowering the North American continental arch. HOUSE (1985) described eight separate extinction events among Devonian ammonoids of which six range from Upper Givetian to Lower Tournaisian (Taghanic, Frasnes, Kellwasser, Enkeberg, Annulata, and Hangenberg Events). Of these events, SEPKOSKI (1986) considered three to be significant (Frasnes or Givetian-Frasnian, Kellwasser or Frasnian-Famennian, Hangenberg or Famennian-Tournaisian; Fig. 9). MCGHEE (1982, 1990) reported 65% extinction among marine placoderm species and 23% among putative freshwater forms during the Frasnian-Famennian extinction episode, though current data suggest an overall placoderm species extinction of 48-51% and a generic extinction of 52-53% (table 1); five out of six placoderm orders survived (Antiarcha, Arthrodira, Petalichthyida, Phyllolepida, Ptyctodontida). MCGHEE commented upon the potential significance of differences in freshwater and marine extinction to the evaluation of causal mechanisms; however, freshwater interpretations for many Old Red Sandstone style sediments have been called into question (e.g. Spitsbergen, GOUJET, 1984a; Escuminac Formation, CHIDIAC, 1989 and VÉZINA, 1991; East Baltic and Podolia, MARK-KURIK, 1991). The Frasnian-Famennian decline was possibly associated with a global event that affected both invertebrate and vertebrate benthic and pelagic communities (MCLAREN, 1988). Causes and timing of this event are currently under debate (for a discussion see MCMILLAN *et al.*, 1988; HOUSE, 1985; SEPKOSKI, 1986). The final decline of placoderms occurred in another association with a major event (Fig. 9). Despite the possibility of a physical cause, it is worthwhile also to evaluate potential biological factors for this final decline. To this end, gnathostome diversity patterns are evaluated.

In the absence of an established phylogeny, MILES (1969) characterized placoderm evolution in terms of specializations related to their life on or just off the bottom. Within arthrodires, he described a succession of competitively superior grades related to improvements in feeding and locomotion. GARDINER (1990) further noted a number of morphological innovations associated with feeding and locomotion. LONG (1990a: 255) evaluated aspects of placoderm evolution in terms of "guiding factors" related to evolutionary trends, although, it should be noted that his

dichotomy of intrinsic ("genetic drift, heterochrony, biophysical constraints") and extrinsic ("environment, abundance of food, predator pressure") factors represents a potential continuum of both proximate and ultimate causal factors.

Placoderms and other Gnathostomes

In one instance among placoderms, choice of taxonomic level (genus versus species) is critical. Ptyctodont generic diversity may represent a misleading indicator of "true" diversity since most members of this taxon are form-genera based on gnathal plates (MILES & YOUNG, 1977). Specific analysis (Fig. 5) provides a more accurate estimate of ptyctodont diversity with 22 out of 31 species in the Frasnian represented by form-genera (*Paleomylus*, *Ptyctodus*, and *Rhynchodus*).

Biological interactions can take several forms including direct competition for resources (e.g. food and nesting sites) and predator-prey relationships. Underlying the potential for interaction are assumptions of geographic overlap and ecological sympatry. The necessity to consider these assumptions is demonstrated below by example. Phyllolepids and rhenanids have a similar dorsoventrally compressed body form suggesting specialization for bottom living. Additionally, petalichthyids have been interpreted as possibly bottom living (DENISON, 1978). The phyllolepids appear as a temporal replacement for the rhenanid and petalichthyid clades (Figs. 4-5); however, if truly marine, it is unlikely that phyllolepids (restricted to Old Red Sandstone marginal marine or estuarine clastic habitats) competitively displaced rhenanids and petalichthyids which inhabited

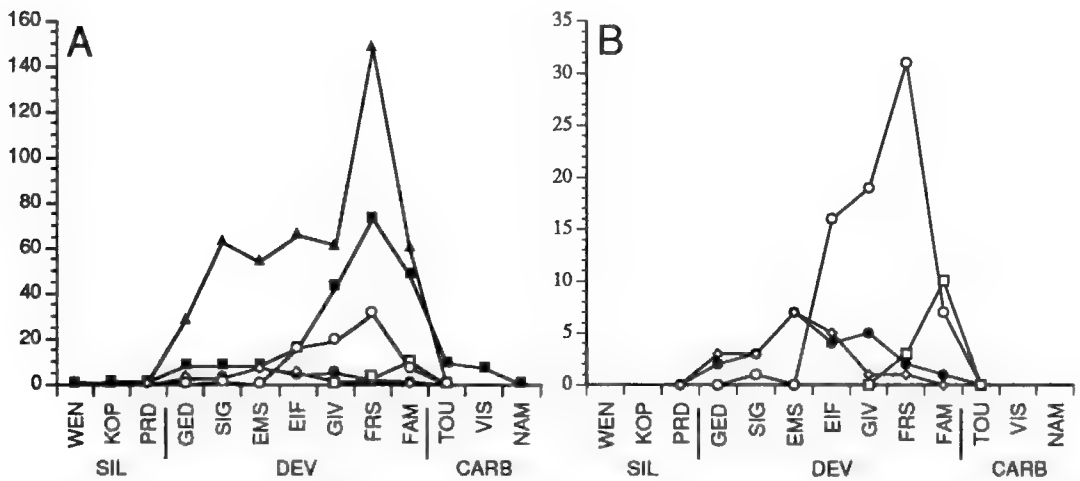

FIG. 5. — Species-level diversity patterns for monophyletic placoderm groups. A, arthrodires (triangles), antiarchs (filled squares), rhenanids (diamonds), petalichthyids (filled circles), phyllolepids (open squares), and ptyctodonts (open circles). B, arthrodires and antiarchs omitted to better demonstrate patterns for low diversity clades.

Courbe des modèles de diversité des espèces pour des groupes monophylétiques de Placodermes. A, arthrodires (triangles), antiarches (carrés pleins), rhénanides (losanges), pétalichthyides (cercles pleins), phyllolépides (carrés), et ptyctodontes (cercles). B, même courbe sans les arthrodires et les antiarches afin de mettre en évidence les modèles de diversité pour des clades peu diversifiés

distinct environments (carbonate and basinal habitats). A globally distributed taxon may interact with other pandemic taxa or regionally with a number of endemic forms. PAN & DINELEY (1988) noted a high level of endemism among placoderms and antiarchs, in particular, suggesting that regional or basinal patterns may represent an appropriate limit of resolution for questions concerning ecological interactions.

PATTERSON & SMITH (1987) demonstrated the potential for pseudo-extinctions with use of paraphyletic groups. Additionally, they noted the potential elongation or truncation of temporal ranges for taxa and possible differences in the timing of peak diversities (contrast SEPKOSKI, 1987). Once a phylogenetic study has been completed, evolutionary trends can be compared and evaluated using monophyletic taxa. Analyses in this study are restricted primarily to monophyletic units as currently understood. The systematics of placoderms is often based on a limited knowledge of morphology and variability. These limits suggest that relationships among placoderms, in contrast to better documented groups, are more susceptible to change with the discovery of new or better material. At present, no higher level monophyletic groups (strict consensus *sensu* SOKAL & ROHLF, 1981) are held in common among the alternative published hypotheses for the relationships of placoderm orders (analysis based on MILES & YOUNG, 1977; DENISON, 1978; GARDINER, 1984; GOUJET, 1984b; FOREY & GARDINER, 1986). Within Placodermi, DENISON (1978) recognized nine orders, with Arthrodira, Phyllolepida, Petalichthyida, Ptyctodontida, Antiarcha, and Rhenanida generally considered to be monophyletic (MILES & YOUNG, 1977; DENISON, 1978; GOUJET, 1984b). The relationships of Stensioellida and Pseudopetalichthyida remain obscure while Acanthothoraci appear to be paraphyletic (GOUJET, 1984b; see YOUNG, 1980, who includes palaeacanthaspids within rhenanids). Figure 4 is a hypothesis of relationships for the majority of taxa addressed here and is based on a number of cladistic analyses (order relationships after GOUJET, 1984b; arthrodiran relationships modified from GARDINER, 1990; CARR, 1991).

Among the arthrodires, the Actinolepidoidei (Fig. 6), a monophyletic group representing MILES' (1969: 144) "actinolepid level of organization," include the Actinolepididae and Wuttagoonaspididae (Fig. 4; MILES & YOUNG, 1977; DENISON, 1978; GOUJET, 1984a). Phlyctaenii (Fig. 6; "phlyctaenaspid level" in part, MILES, 1969: 145) were considered paraphyletic by MILES & DENNIS (1979) and GARDINER (1990), but monophyletic by GOUJET (1984). Included in this clade are Arctaspididae, Arctolepididae, Groenlandaspididae, Phlyctaeniidae, and Tiaraspididae (Fig. 4; GOUJET, 1984a, includes *Tiaraspis* among the Groenlandaspididae). MILES (1969) additionally included Williamsaspididae among the Phlyctaenii, but williamsaspids are here considered basal brachythoracids (Fig. 4; GOUJET, 1984a). Coccosteomorph and pachyosteomorph subgroups (Fig. 6) are considered to be monophyletic. Coccosteomorph arthrodires include Camuropiscidae, Coccosteidae, Pholidosteidae, Plourdosteidae in part, Rhachiosteidae, and Torosteidae (Fig. 4; DENNIS & MILES, 1979; GARDINER, 1990). The "coccosteomorph level" of MILES (1969: 147) further included Buchanosteidae, Euleptaspididae, Gemuendenaspididae, and Holonematidae. These families represent either basal brachythoracid clades or members of basal clades (Fig. 4; "primitive" brachythoracids of LELIÈVRE, 1988; CARR, 1991). Finally, pachyosteomorph arthrodires include the aspinothoracid arthrodires and the Dunkleosteidae (used here as equivalent to the Dinichthyidae *sensu* DENISON, 1978, but excluding *Dinichthys herzeri*, *Gorgonichthys clarki*, *Heintzichthys gouldii*, and *Holdenius holdeni*; contrast STENSIÖ, 1963, and VÉZINA, 1990). MILES (1969) additionally considered Rhachiosteidae (here considered a coccosteomorph)

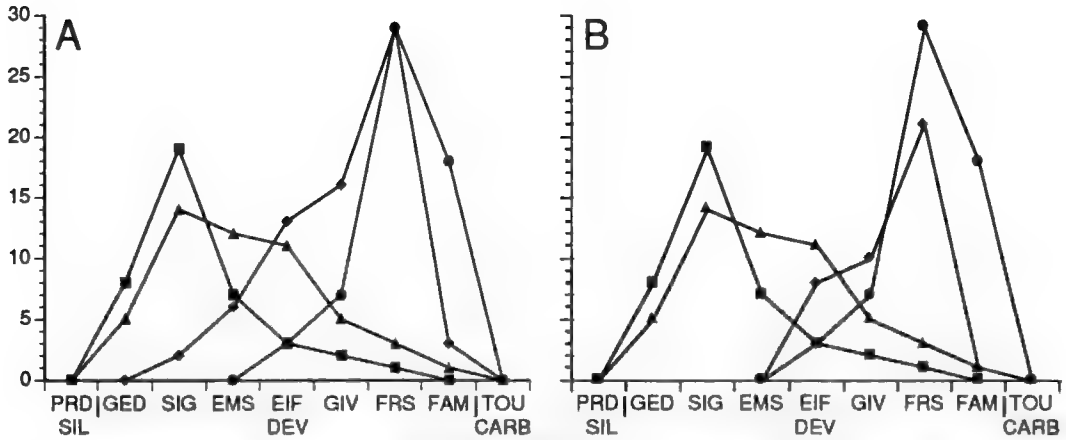

FIG. 6. — A comparison between the generic-level diversity patterns associated with MILES (1969) hypothesis of replacement and the patterns among monophyletic placoderm groups. Note differences in timing of originations and the potential for interactions between groups. A, arthrodiran diversity after MILES (1969), actinolepid level (squares), phlyctaeniid level (triangles), coccosteomorph level (diamonds), and pachyosteomorph level (circles). B, monophyletic groups: Actinolepidoidei (squares), Phlyctaenii (triangles), coccosteomorph arthrodires (diamonds), and pachyosteomorph arthrodires (circles).

Comparaison entre les modèles de la diversité des genres de Placodermes selon l'hypothèse de MILES (1969) et les modèles de groupes monophylétiques de Placodermes. Remarquez les différences entre le temps de l'origine des groupes et leurs relations mutuelles. A, diversité des arthrodires selon MILES (1969) : actinolépides (carrés) ; phlyctaeniides (triangles) ; coccostéomorphes (losanges) et pachyostéomorphes (cercles). B, groupes monophylétiques : Actinolepidoidei (carrés), Phlyctaenii (triangles), coccostéomorphes (losanges) et pachyostéomorphes (cercles).

and Homosteidae ("primitive" brachythoracid, LELIÈVRE, 1988) to be pachyosteomorph arthrodires. Aspinothoracid arthrodires are considered to be monophyletic (MILES & DENNIS, 1979; CARR, 1991; but contrast DENISON, 1984) and here include: Brachydeiridae, Bungartiidae, Leiosteidae, Leptosteidae, Mylostomatidae, Selenosteidae, Titanichthyidae, Trematosteidae, *Gorgonichthys clarki*, *Heintzichthys gouldii*, *Holdenius holdeni* (pers. observ.), and *Dinichthys herzeri* (CARR & HLAVIN, MS).

A generalized sequence of temporal replacement can be seen among the four arthrodiran clades as noted by MILES (1969) and GARDINER (1990); however, a competitive causal relationship is not certain since these patterns represent global data. The pairwise patterns in each case of putative competitive displacement do not demonstrate a clear pattern of ecological replacement ("double-wedge pattern," BENTON, 1987). Additionally, a causal relationship between MILES' (1969) levels should be evaluated in the light of other placoderm and gnathostome taxa considering alternative biotic or abiotic interactions. Actinolepid and phlyctaeniid patterns are not consistent with competitive displacement (Fig. 6) with both groups sharing a similar history of first appearance and peak diversity (Gedinnian and Siegenian respectively). Substage-level analysis demonstrates a possible delay in the timing of phlyctaeniid peak diversity (Upper Siegenian versus Lower Siegenian for the actinolepids). Also, it should be remembered that phlyctaeniids may represent a paraphyletic assemblage needing further evaluation. Coincident with the decline of phlyctaeniids and increase among coccosteomorphs was an increase among antiarchs, ptyctodonts, pachyosteomorphs, and osteichthyans (Figs. 5, 10A). When using monophyletic groups

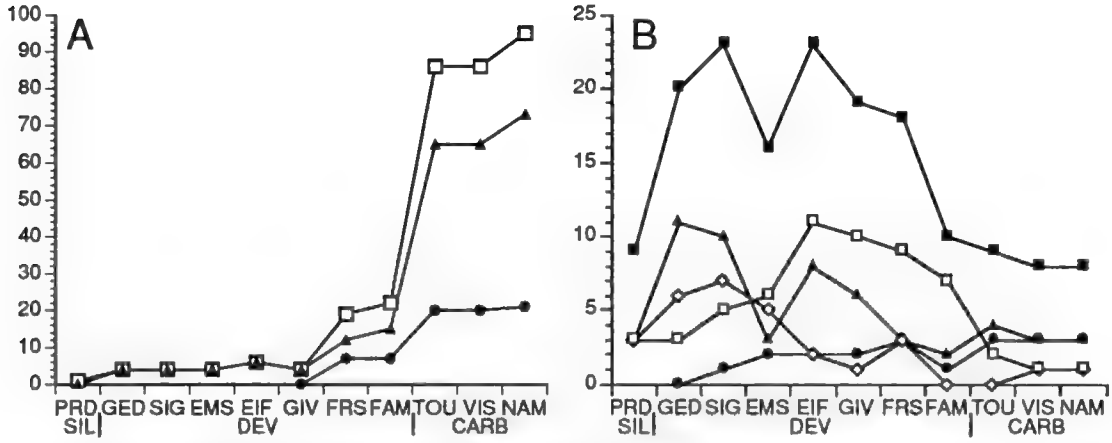

FIG. 7. — Chondrichthyan and acanthodian stage-level generic diversity patterns. Note the end Devonian diversity increase among chondrichthyans and the Middle and Late Devonian decline of acanthodians. A, chondrichthyan diversity: Chondrichthyes (squares), Elasmobranchii (triangles), and Subterbranchialia (circles). B, acanthodian diversity: Acanthodii (filled squares), order Acanthodida (circles), order Climatiidae (triangles), order Ischnacanthida (diamonds), and *incertae sedis* (open squares).

Courbes de modèles de diversité des genres d'Acanthodiens et de Chondrichthyens en fonction des étages géologiques. Remarquez la croissance de la diversité des Chondrichthyens à la fin du Dévonien et le déclin des Acanthodiens pendant le Dévonien moyen et terminal. A, diversité des Chondrichthyens : Chondrichthyes (carrés), Elasmobranchii (triangles), Subterbranchialia (cercles). B, diversité des Acanthodiens : Acanthodii (carrés pleins), ordre des Acanthodida (cercles), ordre des Climatiidae (triangles), ordre des Ischnacanthida (losanges) et incertae sedis *(carrés).*

(Fig. 6B), the decline of phlyctaeniids begins prior to the origin of coccosteomorph arthrodires; however, a comparison of phlyctaeniids and brachythoracid arthrodires is suggestive of a pattern of competitive displacement in analyses carried out at both stage- and substage-level resolution. Generic patterns for pachyosteomorph and coccosteomorph arthrodires are roughly parallel (Fig. 6) and suggest a single pattern differing only in levels of diversity with pachyosteomorphs reaching a higher maximum diversity. In contrast, a substage-level analysis (Fig. 10B) shows the peak diversities of the two clades to be offset which accounts for the bimodal maxima seen in the species- and genus-level Frasnian diversities for placoderms (Fig. 1B). Coccosteomorph arthrodires reached maximum diversity in the Lower Frasnian (which includes the well documented Gogo Formation fauna) with their greatest decline in the Middle Frasnian prior to the Frasnian-Famennian extinction event. This decline does not coincide with known extinctions and suggests a possible biotic cause, although, it is not clear as to which taxa are interacting during this short interval. Pachyosteomorph arthrodires reached peak diversity in the Upper Frasnian prior to the Frasnian-Famennian extinction episode. The conclusions of MILES (1969) and GARDINER (1990), concerning biological interactions among arthrodires, provide a basis for a number of hypotheses that still need regional evaluation and analysis at a finer time scale.

Most placoderms were extinct by the end of the Devonian with antiarchs possibly surviving until the Lower Carboniferous and some arthrodires surviving into the Tournaisian; however, patterns for placoderms and other gnathostomes do not support an ubiquitous effect for the numerous extinction events reported from the Middle and Upper Devonian (HOUSE, 1985; SEPKOSKI, 1986). At the Givetian-Frasnian boundary (Figs. 5-8, 10) few of the major gnathostome clades

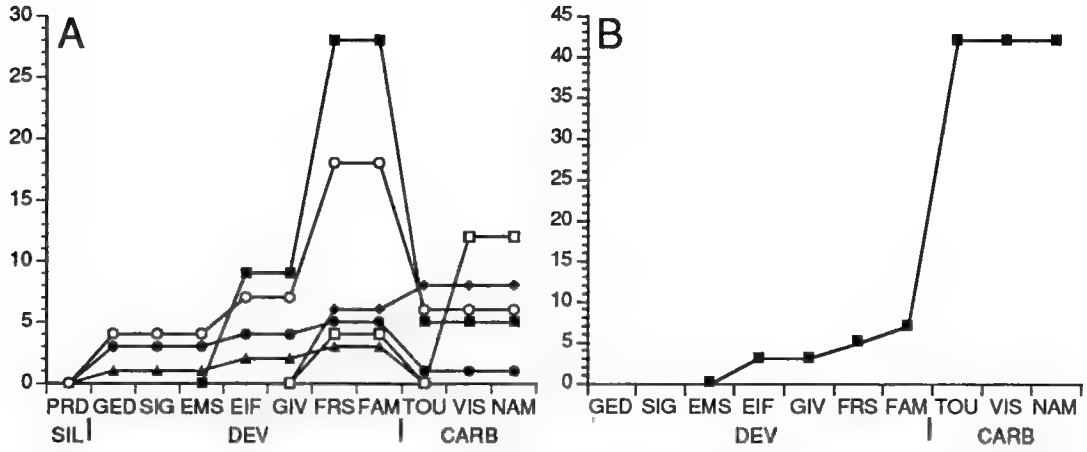

FIG. 8. — Osteichthyan stage-level generic diversity. Note sarcopterygian increasing, stable, and declining diversities associated with the GIV-FRS, FRS-FAM, and FAM-TOU extinction events respectively. A, sarcopterygian diversity: Osteolepidoidea (filled squares), Holoptychoidea (filled circles), Onychodontiformes (triangles), Coelacanthiformes (diamonds), Tetrapoda (open squares), and Dipnoi (open circles). B, actinopterygian generic diversity which parallels the pattern seen among chondrichthyans (Fig. 7A).

Courbe de diversité des Ostéichthyens en fonction des étages géologiques. Remarquez les diversités croissante, stable puis décroissante associées respectivement aux événements d'extinction du Givétien-Frasnien, du Frasnien-Famennien et du Famennien-Tournaisien. A, diversité des Sarcoptérygiens : Osteolepidoidea (carrés pleins), Holoptychoidea (cercles pleins), Onychodontiformes (triangles), Cœlacanthiformes (losanges), Tetrapoda (carrés), Dipnoï (cercles). B, courbe de diversité des genres d'Actinoptérygiens ; elle présente des similitudes avec celle des Chondrichthyens (fig .7A).

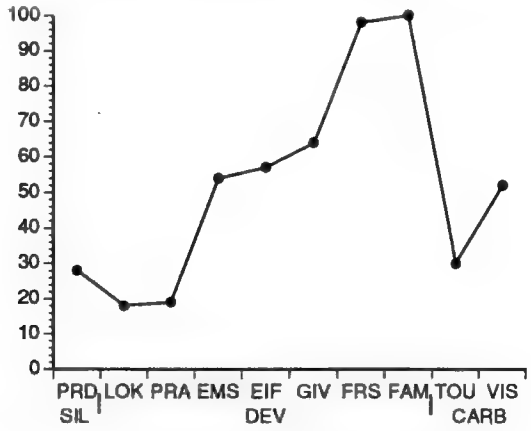

FIG. 9. — Family-level last appearances for all marine animal families taken from SEPKOSKI, 1992.

Courbe de la dernière présence signalée au niveau de la famille des animaux marins, d'après SEPKOSKI, 1992.

demonstrate a generic decline except petalichthyids, whose low diversity prevents meaningful analysis, and acanthodians. Several clades demonstrate increases in the number of genera (actinopterygians, sarcopterygians, chondrichthyans, arthrodires, and phyllolepids) while remaining

clades of gnathostomes maintain stable levels. The Frasnian-Famennian boundary coincides with declines in all placoderm orders discussed here, but one (low diversity phyllolepids), and a continuing decline in acanthodians. At the Famennian-Tournaisian boundary, there was a major diversity increase for chondrichthyans and actinopterygians. Coincident with this increase was a decline among rhipidistians, dipnoans, and remaining placoderms. McGhee (1988) noted the importance of temporal resolution in evaluating the timing of events in the fossil record; however, resolution problems still exist and the relative timing of the osteichthyan radiation and placoderm decline is not clear. This is demonstrated by the epoch level resolution for sarcopterygian diversity which limits any analysis of the Frasnian-Famennian extinction event for this clade.

Williams (1990) provided direct evidence for the interaction among Late Famennian gnathostomes within the Cleveland Shale fauna. He documented evidence for predator-prey relationships among piscivorous members of the fauna concluding (p. 287) simply that "the big fish ate the little ones," suggesting a general absence of prey selectivity. Additionally, there was potential competition among durophages with independent evolution of durophagous feeding structures in placoderms (e.g. Ptyctodontida, Mylostomatidae), dipnoans, and chondrichthyans (e.g. *Orodus*). By the end of the Mississippian, a number of holocephalan and elasmobranch durophages had evolved (Zangerl, 1981; Carroll, 1988). Additionally, Vermeij (1987) noted a doubling of marine durophagous families of eurypterid and crustacean arthropods, cephalopod molluscs, and vertebrates between the Middle and Upper Devonian.

The above findings suggest that the Frasnian-Famennian extinction episode was critical in the initial evolution of actinopterygians and chondrichthyans providing a so-called "opportunity

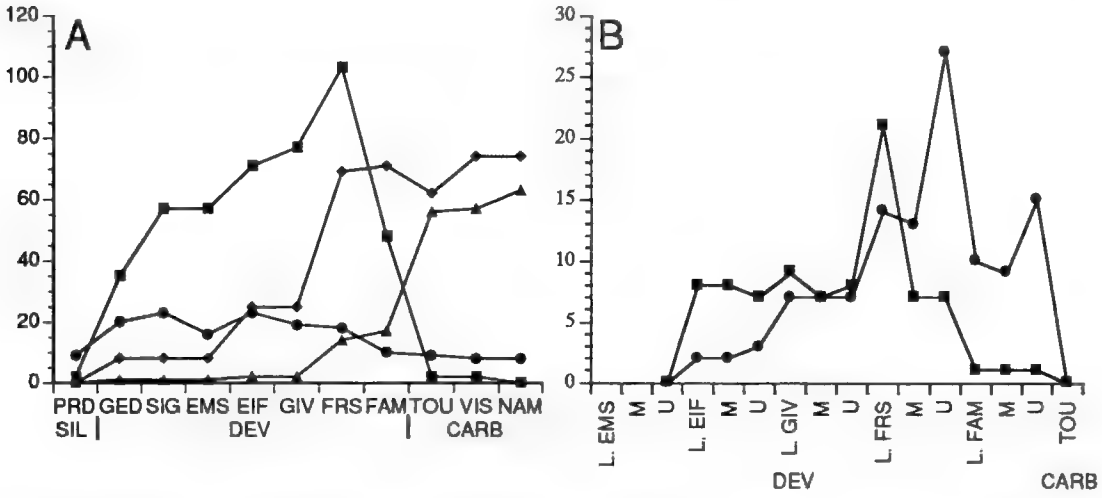

Fig. 10. — A, a comparison of stage-level generic diversity for major gnathostome clades: placoderms (squares), acanthodians (circles), osteichthyans (diamonds), and chondrichthyans (triangles). B, eubrachythoracid substage-level generic diversity: coccosteomorph arthrodires (squares) and pachyosteomorph arthrodires (circles). Note the decline of coccosteomorph arthrodires prior to the FRS-FAM extinction event.

A, Courbe de comparaison de la diversité des groupes majeurs de Gnathostomes en fonction des étages géologiques : Placodermes (carrés), acanthodiens (cercles), osteichthyens (losanges) et chondrichthyens (triangles). B, même courbe pour les Eubrachythoraci en fonction des sous-étages. Arthrodires coccostéomorphes (carrés), Arthrodires pachyostéomorphes (cercles). Remarquez le déclin des coccosteomorphes à partir de l'événement Frasnien-Famennien.

or open window" for their early radiation. Within the Famennian there is clear evidence of direct predator-prey interactions and apparent competition for other resources. Much of placoderm evolution revolved around specializations on a basic plan with retention of a relatively primitive placoderm suspensorium and vertebrate locomotor pattern (see discussion below). In contrast, chondrichthyans and actinopterygians evolved a number of innovations associated with feeding and locomotion which have been well documented (e.g. SCHAEFFER, 1975; ZANGERL, 1981; LAUDER, 1982; WEBB, 1982; LUND *et al.*, 1984). With the rapid increase in diversity among actinopterygians and chondrichthyans after the Frasnian-Famennian extinction event, it is proposed that these forms may have competitively displaced contemporaneous placoderms; however, the suggested presence of a major Famennian-Tournaisian extinction event is consistent with a model of opportunistic replacement by surviving actinopterygians and chondrichthyans. Tests of this hypothesis must await detailed basinal and regional faunal analyses. Current field work and review of the open basin faunas associated with the Catskill Delta and Michigan Basin may shed light on the history and extinction of placoderms in the Upper Devonian.

PACHYOSTEOMORPH DIVERSITY PATTERNS

Among pachyosteomorph arthrodires, the aspinothoracid subclade accounts for 50% of all described pachyosteomorph species. Remaining pachyosteomorphs comprise the Dunkleosteidae (and possibly Panxiosteidae). Aspinothoracid arthrodires first appeared in the Upper Givetian with an apparent increase in species diversity until the Frasnian-Famennian extinction episode. The Laurasian record for aspinothoracids includes Lagerstätten on both sides of the extinction episode suggesting the Frasnian peak does not represent a sampling bias. Each Lagerstätten (Upper Frasnian Kellwasserkalk of the *Manticoceras* beds of Bad Wildungen, Germany, and Late Famennian Cleveland Shale, northern Ohio, USA) represents similar deep water sedimentary environments which suggest potentially similar taphonomic processes. There is no data available for Devonian stage-level sediment volumes and surface exposures. RONOV (1980) provides series-level global data which indicates equivalent sediment volumes and areas for the Middle and Upper Devonian. However, differences in estimated duration (HARLAND *et al.*, 1989) suggest a potential sampling bias in favor of Frasnian sediments, but SEPKOSKI (1991) has pointed out that ages for the Devonian stage boundaries are poorly constrained and time averaging may be omitted until better estimates are available (HARLAND *et al.*, 1989, note a high level of uncertainty for estimating the lower boundary date for each Upper Devonian stage. They note an error of plus or minus an amount equal to or greater than the duration of the stage). During the Famennian, there was little if any numerical recovery of diversity at the species level following the Frasnian-Famennian extinction event. However, among arthrodires there was a secondary radiation associated with habitat utilization, feeding structures, food acquisition, and locomotor patterns. Aspects of this radiation are seen clearly in the Late Famennian Cleveland Shale fauna of North America with its morphologically diverse assemblage of aspinothoracid arthrodires. The question then arises: what might account for this apparent increase in pachyosteomorph diversity? Two major adaptive aspects of the phenotype are associated with feeding and locomotion. It is difficult to determine the prey of most placoderms, but the biological role, in mechanical terms, of the structures associated with feeding and locomotion can be evaluated. An analysis of potential functional consequences of evolutionary changes in feeding morphologies must consider both

architectural and physiological aspects of muscle. Recent advances in the understanding of feeding mechanics necessitate a more thorough consideration of the components involved and the potential trade-offs associated with evolutionary modification.

Feeding

MILES (1969) and SCHAEFFER (1975) discussed major trends in feeding mechanisms within placoderms and gnathostomes respectively. Placoderms possess an autostylic jaw suspensorium (Fig. 11; MILES, 1969) with the hyomandibula (Hm) supporting the submarginal plate (GOUJET, 1984a, b; contrast YOUNG, 1980, 1986). The palatoquadrate is fused to the dermal cheek (suborbital, SO, and postsuborbital plates, Fig. 11) providing support for the jaw articulation. An adductor mandibulae muscle originates from the palatoquadrate and the medial surface of the suborbital plate (GOUJET, 1984b) and inserts along the lateral surface of the lower jaw (IG, Fig. 11), attaching either to the non-masticatory portion of the inferognathal plate, when present, and/or to Meckel's cartilage (Mk, Fig. 11). The dermal inferognathal plate (Figs. 11, 12) consists of an anterior occlusal region and posterior non-masticatory or "blade" portion. The non-masticatory ossified portion varies in arthrodires (CARR, 1991) from a short ventrally grooved structure capping Meckel's cartilage (Fig. 12A) to a single enlarged lamina medial to Meckel's cartilage (Fig. 12B-G).

MILES (1969: 149) considered main brachythoracid trends to have been associated with increasing the gape and "effective use" of gnathal elements (increased inferognathal length, large nuchal gap, functional articulation of the head). What constitutes "effective use" depends upon the role required of the gnathal elements (e.g. durophages increase crushing forces while some piscivores increase closing velocity to let the strike facilitate prey capture). MILES (1969) characterized the inferognathal as a third class lever, arguing that evolution of the brachythoracid feeding

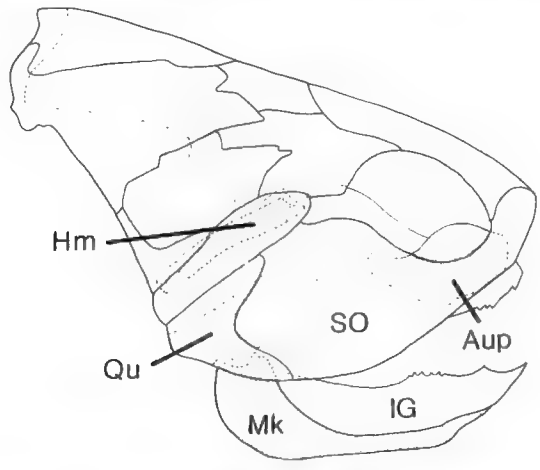

FIG. 11. — Lateral view of *Coccosteus* sp., showing autostylic jaw suspension of arthrodires, from GARDINER, 1984. Structures deep to dermal bones are drawn with a dashed outline. Cartilaginous structures are stippled.

Vue latérale de Coccosteus *sp., montrant la supension autostylique des mâchoires, d'après* GARDINER, *1984. Les structures périchondrales profondes sont indiquées par une trame. Les structures cartilagineuses sont en pointillé.*

mechanism balanced an anterior muscular insertion (improved in-force) with improved gape. For a given mass of muscle, a more distal placement and increased velocity associated with enlarged gape are potentially in conflict (inferognathal velocity is dependent in part on the force available for mandibular acceleration which reflects muscle fiber organization and rotational inertial effects). It is not clear what constitutes MILES' (1969) concept of elongation for the lower jaw. The ossified "blade" does not extend from the articular to the occlusal surface in all arthrodires. Elongation may be used to describe the lengthening of the "blade" to reach the articular or to describe the relative increase in length for the entire lower jaw (articular to symphysis). It appears that both forms of elongation have occurred among arthrodires. A complete "blade", present from the articular to the occlusal region, appears to be a synapomorphy of eubrachythoracid arthrodires and *Homostius* (CARR, 1991). A visual inspection of the relative lengths between the lower jaw (or the length between the quadrate on the postsuborbital plate and the position of the posterior superognathal on the suborbital) and a longitudinal measure for the head shield (e.g. orbit to glenoid condyle) suggests that pachyosteomorph arthrodires have developed an elongated lower jaw. Finally, MILES' summary does not explain the presence of forms with a reduced blade restricting muscular insertion posteriorly (e.g. *Hadrosteus*, Fig. 12F).

In a rotational gnathal system (Eq. 1; ALEXANDER, 1968), the out-moment is equal to the in-moment.

$$F_o\ L_o = F_i\ L_i \text{ (Eq. 1)}$$
$$F_o = (\ F_i\ L_i\ )\ /\ L_o \text{ (Eq. 2)}$$

More effective out-force application (Eq. 2) can be achieved in a number of ways.

(1) The out-force moment arm (L_o) can be reduced either by applying forces only to posterior aspects of the occlusal surface or by shortening the inferognathal (as seen in *Mylostoma*, DENISON, 1978, Fig. 79, or in *Oxyosteus*, STENSIÖ, 1963, Pl. 55, Figs. 4, 5).

(2) Muscle force (F_i) can be increased by increasing the mass of the muscle (GANS & DE VREE, 1987; GANS & GAUNT, 1991). Addition of muscle mass is constrained by restrictions on muscle packing (*i.e.* available space and fiber orientation) and metabolic costs.

(3) Finally, out-forces can be affected through modification of inferognathal shape with development of a coronoid process (as noted by MILES, 1969, and among placoderms seen only in *Brachyosteus dietrichi*, Fig. 12D). This either accommodates phylogenetic shifts in the angle between lines of muscle action and lever action or simply provides increased area for the insertion surface. MILES' (1969) proposal - a simple anterior shift of muscle insertion (increased L_i) - fails to recognize that an increase in moment arm is paid for by a reduction in muscle force (GANS, 1988; GANS & GAUNT, 1991). Placement of the adductor muscle closer to the joint does minimize the rotational inertia (GANS, 1988).

An alternative to MILES' hypothesis (elongation of inferognathals to increase in-force moment arm and gape) includes (1) inferognathal elongation to increase gape, (2) elongation and reduction of inertial effects to increase closure velocity (note that power increases with increased muscle force, but not with changes of in-force moment arm), and (3) ossification of the inferognathal plate, from the articular to the symphysis, to stabilize and strengthen the lower jaw. Since power does not increase and out-forces decrease with the increase of jaw length (out-force moment arm), other mechanisms for enhancement of the bite might be predicted based on feeding strategy. Development of an ossified blade provides a strengthened and stable insertion for a

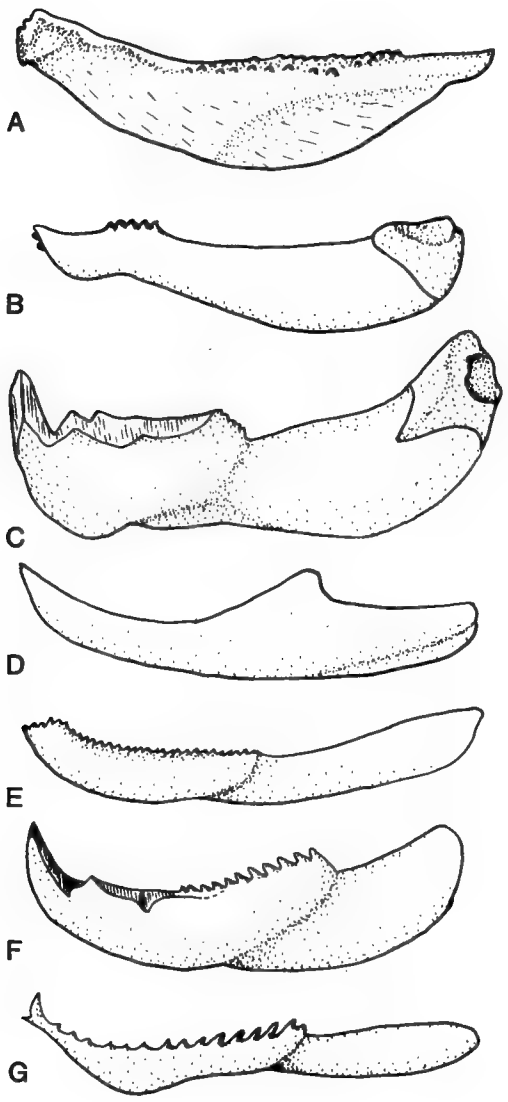

FIG. 12. — Inferognathal plates in lateral view. A-G redrawn from GROSS, 1967. A, indeterminate dolichothoracid, × 0.96. B, *Pholidosteus friedeli*, × 1.16. C, *Dunkleosteus terrelli*, × 0.24. D, *Brachyosteus dietrichi*, × 1.48. E, *Rhinosteus tuberculatus*, × 1.6. F, *Hadrosteus rapax*, × 0.44. G, *Diplognathus mirabilis*, × 0.38.

Plaque gnathale inférieure en vue latérale. A-G d'après GROSS, 1967. A, dolichothoracide indet., × 0,96. B, Pholidosteus friedeli, *× 1,16. C,* Dunkleosteus terrelli, *× 0,24. D,* Brachyosteus dietrichi, *× 1,48. E,* Rhinosteus tuberculatus, *× 1,6. F,* Hadrosteus rapax, *× 0,44. G,* Diplognathus mirabilis, *× 0,38.*

potentially larger adductor muscle mass with a resulting increase in in-force. Elongation of the blade in placoderms may have represented a consequence of the relationship between the suspensorium and dermal cheek in placoderms. Fusion of the palatoquadrate and dermal skeleton along with limited cheek mobility or fusion of the cheek to the head shield restricted expansion of the muscles upon contraction. An elongated blade provides a potential attachment for a larger anterior-posterior muscle mass, although, changes in fiber orientation may provide similar results (equivalence, GANS & GAUNT, 1991). In contrast, the proportionally short blade of *Hadrosteus* (Fig. 12F) and *Diplognathus* (Fig. 12G) suggests specialization for rapid closure. The presence of elongated denticles along the occlusal surface in these genera, especially *Diplognathus*, is consistent with a strategy of taking whole prey with little or no buccal reduction after capture. A common pattern among pachyosteomorph piscivores (e.g. *Dunkleosteus*, Fig. 12C, *Heintzichthys*, and *Gorgonichthys*) was development of an anterior cusp maximizing the stress (force per unit area) imposed upon prey and providing sufficient shear forces to pierce dermal bone or the exoskeleton of invertebrates. The presence of a single inferognathal ossification provided resistance to bending forces generated by an impaling action of the anterior cusps. Selenosteids (ØRVIG, 1980a, Figs. 52-56) and *Bungartius* (DENISON, 1978, Fig. 81) similarly developed a prominent denticle along the occlusal surface. Long occlusal surfaces (e.g. up to 66% of inferognathal length in *Hadrosteus*) provided posteriorly displaced occlusal surfaces with an increased range of out-forces for crushing, partitioning, or grasping while maintaining an enlarged gape (occlusal surfaces are close to 50% among dunkleosteids, selenosteids, *Heintzichthys*, and *Holdenius*; similar proportions are found in eubrachythoracids in general). Development of large orbits, seen in a number of aspinothoracid and coccosteomorph arthrodires, would not have been a limiting factor in development of an enlarged gape and muscle insertion as suggested by MILES (1969).

Within pachyosteomorph arthrodires there was a morphological diversification of occlusal surfaces. In this group were specializations for durophagy (e.g. *Mylostoma*, *Paramylostoma*), piscivory (e.g. *Dunkleosteus*, *Gorgonichthys*, *Heintzichthys*), and possibly planktivory (*Titanichthys*, DENISON, 1978). Occlusal diversification also occurred independently within the coccosteomorph arthrodires, although, to a lesser degree.

Locomotion

Several trends within eubrachythoracid (pachyosteomorph) evolution appear to involve aspects of locomotion. The post-thoracic region is known only for a few placoderms. In all these cases and those in which there is partial preservation of the vertebral column, the notochord is unrestricted. The shape of the caudal fin can be described as heterocercal but, unlike sharks, there is no direct evidence for an enlarged dorsal lobe and the ventral lobe is small and supported only by elongated haemal arches. WILLIAMS (pers. comm.) has reported the presence of ceratotrichia in the pectoral fin of an unidentified aspinothoracid and a specimen of *Dunkleosteus* suggesting the possibility of expanded arthrodiran fin profiles beyond their currently known limits. Hydrodynamically, the caudal fin has a low aspect ratio (span/chord), resulting in relative decreased thrust. The mode of locomotion was most likely anguilliform or eel-like undulation. Associated with this type of locomotion in extant fishes are:

(1) slow speed;
(2) a lack of rapid acceleration;

(3) and decreased agility (referring to the rate of movement).

Unlike extant anguilliform swimmers and suggestive, in part, of subcarangiform locomotion (LINDSEY, 1978) was the inflexibility of the anterior third of the body along with a concentration of mass anteriorly (LINDSEY 1978, table 2, characterizes subcarangiform mode as: similar to anguilliform with reduced anterior undulations; fusiform body; "body tends to be heavier and more rounded anteriorly"; deep caudal peduncle; low aspect ratio caudal fin; flexible caudal fin with straight posterior margin or indented margin and intrinsic musculature). Effects of these two parameters (flexibility, mass), concentrated undulations to the posterior two thirds of the body and limited anterior yaw. Extant subcarangiform fishes often reduce the effect of yaw through an enhancement of the lateral profile, which additionally shifts the center of gravity forward (similar lateral compression is seen in Brachydeiridae). To go beyond these simple observations is difficult since the hydrodynamics and range of responses in extant anguilliform swimmers are still poorly understood. Associated with changes in arthrodiran caudal locomotion were modifications in the pectoral fins improving maneuverability.

Pectoral fins are difficult to evaluate in placoderms, but there are some basic principles that can be assessed (for a review of hydrodynamics see BONE and MARSHALL, 1982). In fishes, fins can be oriented in any position from horizontal to vertical with the latter case operating in a drag regime, analogous to using a boat oar. Horizontal fins can be either passive or active lift structures with the amount of lift varied by shifting the angle of attack. An active lift system is one in which lift is used to generate forward thrust, e.g. as seen in extant holocephalans (LINDSEY, 1978) and possibly among ptyctodonts and rhenanids (MILES, 1969, argued that the heavily scaled and narrow based fins of gemuendinids were incapable of generating forward thrust, but were used in burying the animal in sediment; however, these two functions are not mutually exclusive). In pachyosteomorph arthrodires, the fin was a nearly horizontal lift structure in which the fin base was lengthened with a concurrent increase in the number of fin basals (cr.art, Fig. 13; WESTOLL, 1958; STENSIÖ, 1959). Outgroups had a narrow based fin with fewer basals (Fig. 13A; STENSIÖ, 1959; GOUJET, 1984a, YOUNG & ZHANG, 1992). Fin basals articulated

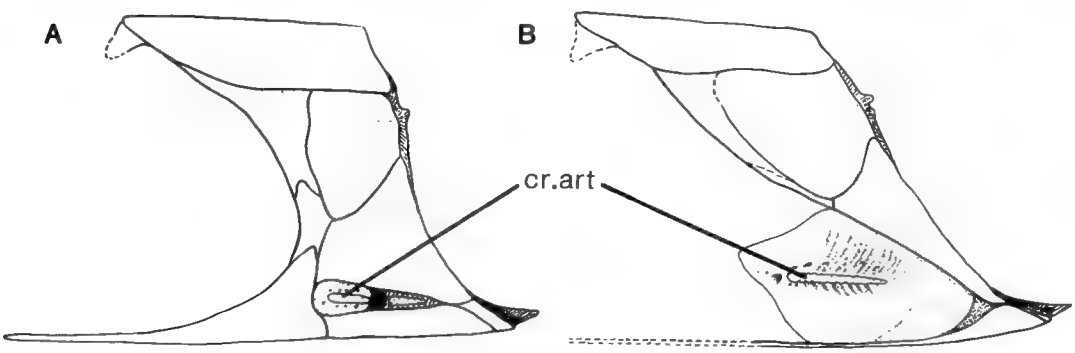

FIG. 13. — A comparison of narrow and broad based pectoral fins. A, *Pholidosteus* sp.; B, *Rhinosteus parvulus*, redrawn from STENSIÖ, 1959.

Comparaison entre des nageoires pectorales étroites et larges. A, Pholidosteus *sp.* ; *B,* Rhinosteus parvulus, *d'après* STENSIÖ, *1959.*

individually with the pectoral girdle, typically without fusion of these structures into more complex pro-, meso-, or metapterygia. A simple metapterygium is known in several forms. In *Heintzichthys gouldii*, the metapterygium has a posteriorly placed flange (CARR, 1991, Fig. 16), which may have functioned as a site for muscle attachment for use in fin retraction or in altering fin camber (anteroposterior curvature). Retraction allows for changes in geometry of the fin with differing velocities (retraction is not seen in extant sharks with a broad based fin). Additionally, there was increased surface area on the scapulocoracoid for both dorsal and ventral muscle attachments (Fig. 13B). This type of fin potentially could increase maneuverability through the use of differential lift or to reduce surface friction at faster swimming speeds for which less lift is required. Another possibility is that seen in extant holocephalans where forward thrust is provided by pectoral fin undulations. In these forms, a forward thrust equal or greater than caudal thrust can be generated (LINDSEY, 1978). In aspinothoracids, choice between these two options would be purely speculative. Decision requires information about the fin span; however, increased musculature and lack of fusion might suggest the possibility of active lift in some forms. On the other hand, distally tapered basals in *Heintzichthys gouldii* (CARR, 1991, Fig. 16A, B) would suggest passive lift in this form.

Shortening of the thoracic shield represents another trend potentially associated with locomotion (Fig. 14). An enclosed trunk was a primitive characteristic of placoderms (MILES & YOUNG, 1977; GOUJET, 1984b), with antiarchs and arthrodires possessing a relatively elongated thoracic shield posterior to the pectoral fenestra. Early evolution of head and thoracic shields, as noted above, may have been associated with modification of primitive anguilliform swimming to minimize yaw associated with undulatory locomotion thereby limiting energy loss (WEBB, 1982). Arthrodires eventually lost body scales increasing flexibility. In *Coccosteus cuspidatus* (Fig. 3F), nearly 38% of the total body length is inflexible to lateral bending. The starting point for the generation of a propulsive body wave to accelerate a body of water was therefore displaced posteriorly. WESTOLL (1958) and MILES (1969) separately suggested shortening of the thoracic shield and recruitment of additional body segments to increase propulsive capability through the development of large amplitude waves; however, it is the rate that the water is shed which is proportional to thrust. Most bony fishes and lamnid sharks, in contrast, increase the propulsive effect by shortening the length of the body involved in the propulsive wave and increase the aspect ratio or lateral profile of the tail along with oscillatory rate. In many cases among arthrodires, the shortening of the thoracic shield is restricted to the lateral pectoral embayments and median dorsal plate (MD, Fig. 14). The posterior ventrolateral plates (PVL, Fig. 14) extend posteriorly to a position equal to that in forms with a closed pectoral fenestra. This would limit undulations to regions equivalent to forms without reduction. In forms with shortening of the lateral and midline portions of the thoracic shield (e.g. *Homostius*, *Heterosteus*, rhenanids, and ptyctodonts which are interpreted as bottom dwellers), the reduction may have been associated with improved maneuverability in turning. Overlap and interdigitation between plates of the dermal head shield also provided a stable platform associated with development of the craniothoracic articulation, although, the articulation is lost in brachydeirids and of questionable function in *Holonema* (LELIÈVRE *et al.*, 1990). The articulation was further modified in brachythoracid arthrodires by transverse occipital thickening of the head shield (GOUJET, 1984b). Shortening of thoracic shield reduces anterior body mass. Within aspinothoracid arthrodires this was

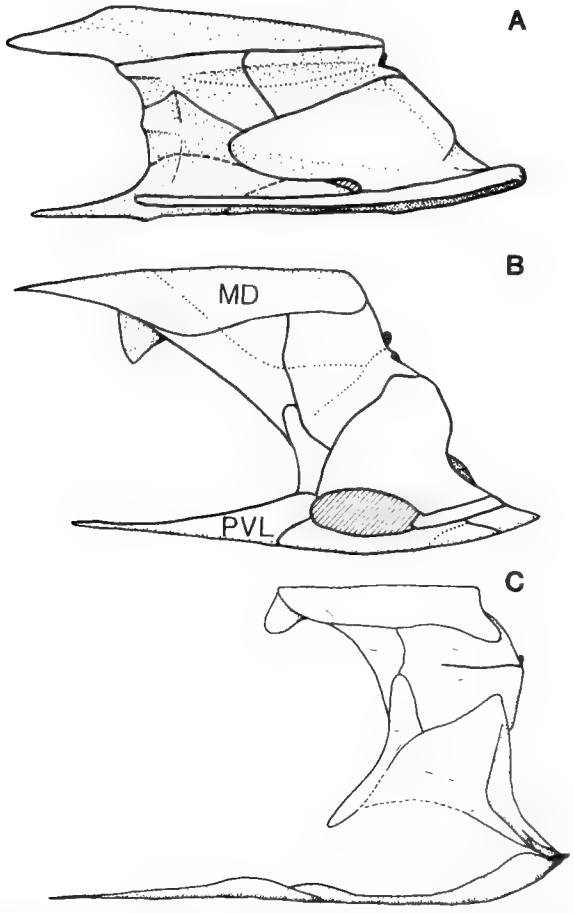

FIG. 14. — Lateral view of three arthrodiran thoracic shields showing the shortening of lateral and dorsal portions: A, *Dicksonosteus arcticus*, a phlyctaeniid redrawn from GOUJET, 1984a. B, *Coccosteus cuspidatus*, a coccosteomorph arthrodire redrawn from MILES & WESTOLL, 1968; C, *Heintzichthys gouldii*, an aspinothoracid arthrodire redrawn from CARR, 1991.

Vue latérale de trois cuirasses thoraciques d'arthrodire montrant le raccourcissement des régions dorsales et latérales : A, Dicksonosteus arcticus, *un phlyctaeniide d'après GOUJET, 1984a. B,* Coccosteus cuspidatus, *un coccostéomorphe d'après MILES & WESTOLL, 1968 ; C,* Heintzichthys gouldii, *un Arthrodire aspinothoracide d'après CARR, 1991.*

paralleled by a reduction in the head shield and may be related to changes in static buoyancy associated with sustained or prolonged swimming (HOAR & RANDALL, 1978: xiii).

Orbits

Many extant mesopelagic fish, which live between 200 to 1000 m, and benthic fishes living above 1000 m have large eyes (NIKOLSKY, 1978; NICOL, 1989). Large eyes are correlated with increased visual acuity in diurnal fishes or increased sensitivity in crepuscular and nocturnal

fishes (WALLS, 1942; NICOL, 1989). Associated with this increase in both relative and absolute sizes is a concordant change in pupil size (NICOL, 1989). Since the intensity of light varies as the square of the distance traveled, an increase in eye diameter would require an enlargement of the aperture to maintain image intensity on the retina. This relationship is found within both elasmobranchs and osteichthyans (NICOL, 1989) suggesting a common, although independently derived (GRUBER & COHEN, 1978), pattern among gnathostomes.

Within aspinothoracids, large eyes developed independently several times (Figs. 15B, 16A). This independence is supported, in part, by differences in the head shield to accommodate increased orbit size (e.g. trematosteids show an elongation of the preorbital plates with increased orbit size whereas European selenosteids, Fig. 15B, have elongated central plates with marginals incorporated into the orbital border). *Heintzichthys gouldii* (Fig. 16A), in contrast to *Dunkleosteus terrelli* (Figs. 15A, 16B-C), shows an increase in relative and absolute orbit size. The internal curvature on the sclerotic of *Heintzichthys gouldii* further supports this difference in size. Additionally, the diameter of the aperture has increased, so that the pupil could have been bigger. Large orbits may suggest adaptation for improved visual acuity or low light intensity (MILES, 1969) either at night or deeper in the ocean. A similar pattern of orbit size is seen within coccosteomorph arthrodires (compare *Pholidosteus* with *Latocamurus*).

In summary, the pattern of species diversity for aspinothoracid arthrodires suggests an apparent increase for this group in the late Middle and early Late Devonian. Coincident with this increase are a number of morphological changes related to feeding, locomotion, and food acquisition. In evaluating these changes relative to other gnathostomes, the placoderms in general have retained their primitive suspensorium and locomotor pattern; however, the eubrachythoracid and in particular the aspinothoracid arthrodires demonstrate a number of specialized modifications on this basic pattern.

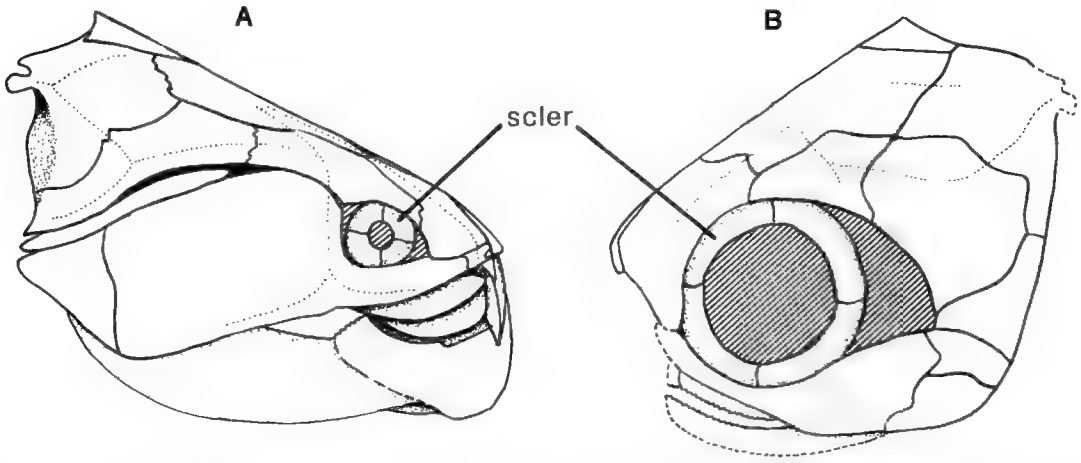

FIG. 15. — A comparison of the relative size for sclerotic rings redrawn from STENSIÖ, 1963. A, *Dunkleosteus terrelli*, × 0.07. B, *Microsteus angusticeps*, × 1.1.

Comparaison de la taille relative des anneaux sclérotiques, d'après STENSIÖ, 1963. A, Dunkleosteus terrelli, *× 0,07. B,* Microsteus angusticeps, *× 1,1.*

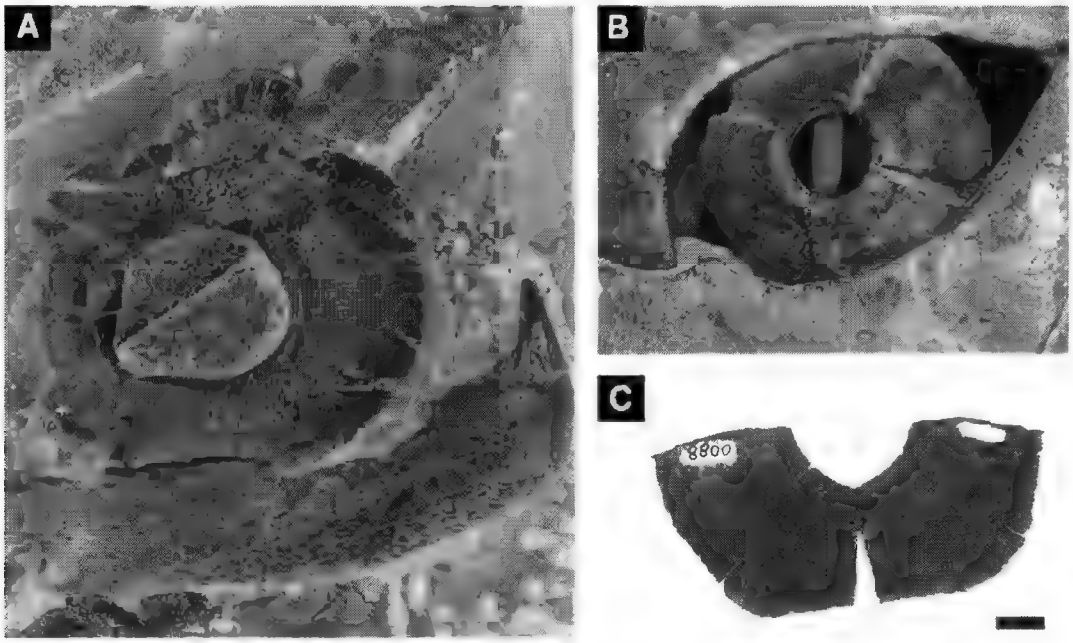

FIG. 16. — *Heintzichthys gouldii*, A, right sclerotic ring and inferognathal (CMNH 7308). *Dunkleosteus terrelli*, B, partially reconstructed and mounted left sclerotic ring (CMNH 6090). C, incomplete sclerotic ring (CMNH 8800). The above sclerotics are reproduced to the same scale. Note the absolute and relative increase in orbit size for *Heintzichthys* a much smaller arthrodire. Scale bar: 1 cm.

Heintzichthys gouldii, *A, anneau sclérotique droit et inférognathal (CMNH 7308).* Dunkleosteus terrelli, *B, anneau sclérotique gauche reconstruit (CMNH 6090). C, anneau sclérotique incomplet (CMNH 8800). Les figures A-C sont à la même échelle. Remarquez la croissance absolue et relative de la taille de l'orbite pour* Heintzichthys, *le plus petit arthrodire des deux. Échelle : 1 cm.*

CONCLUSION

The pattern of placoderm global diversity suggests a number of hypotheses concerning their ecology and evolution (see above; MILES, 1969; LONG, 1990a; GARDINER, 1990) however, tests of these hypotheses should additionally consider both basinal and regional patterns. Existing data, allow determination of critical times of origination and extinction and potential causal interactions which suggest areas for additional study (e.g. diversity shifts at the Middle-Upper Devonian transition associated with major facies changes suggesting questions of emigration versus extinction). The current study suggests that stratigraphic analysis down to substage level is required for the recognition of patterns among placoderm subclades. At present, taxonomic and temporal resolution for individual taxa is less critical with utilization of all available data providing the best picture. To address remaining questions, much work is needed exploring western North American cratonic deposits. Recent field work in Indochina (e.g. BLIECK *et al.*, 1984; JANVIER *et al.*, 1987; THANH & JANVIER, 1987; LONG *et al.*, 1990), Africa and Middle East

(e.g. LELIÈVRE, 1984a, b; 1988; LELIÈVRE *et al.*, 1981), Australia (e.g. MILES & DENNIS, 1979; YOUNG, 1988a; LONG, 1990b), Antarctica (e.g. YOUNG, 1988b) and South America (e.g. GOUJET *et al.*, 1985) have added significantly to our understanding of diversity and biogeography among gnathostomes. Additionally, specific critical periods in gnathostome evolution (e.g. Famennian-Tournaisian) require active exploration with known Devonian localities needing renewed interest. A number of Middle and Upper Devonian Michigan Basin invertebrate localities have been collected extensively (EHLERS & KESLING, 1970) with few or no records of fossil fishes. In a two week field period (Antrim Shale Formation and Traverse Group, Summer 1991), I collected remains belonging to 12 genera of gnathostomes, new to the basin, along with three genera which represent extensions of known ranges. The Middle to Late Paleozoic represents a key period in the evolutionary history of gnathostomes and a renewed interest in field work offers much potential.

The early placoderms show a trend toward solidification of the head and thoracic shields associated with the origin and enhancement of the cranio-thoracic articulation and possible modification of anguilliform locomotion. Arthrodires reduced body scales, perhaps increasing maneuverability. Within aspinothoracid arthrodires, secondary locomotor trends included further development of pectoral fin maneuverability and lift along with mass reduction through lateral shortening of the thoracic shield and thinning of the dermal bone. If initial gains in mass were associated with inertial stabilization in a modification of anguilliform locomotion, secondary loss would suggest further modifications away from a purely anguilliform style of locomotion. However, there is no preservation of post-thoracic anatomy among aspinothoracid arthrodires to confirm this relationship. Several forms (brachydeirids) showed lateral compression which would minimize yaw associated with loss of anterior mass. Pachyosteomorph arthrodires developed the widest range of feeding modifications on the unique placoderm pattern of fixing the suspensorium to the dermal skeleton. This pattern may have been a limiting factor in their evolution and competition with other evolving gnathostomes, despite the evolution of a wide diversity of gnathal morphologies among pachyosteomorph arthrodires along with mechanical specializations. Ossification of the inferognathal blade (a brachythoracid character) provided attachment for enlarged adductor musculature. A number of taxa developed elongated inferognathals characterized by increased bite velocity and modification of the anterior cusp to impale prey. Large occlusal surfaces permitted a wide range of potential out-force for crushing or partitioning of food. Specialized durophages (e.g. *Mylostoma*) reduced the occlusal portion of the inferognathal concentrating crushing surfaces posteriorly. Enlarged orbits were achieved independently in a number of arthrodire groups and are correlated with either increased acuity or specialization for low light intensity.

In contrast to the generalized perception of placoderms as sluggish modified benthic fishes, the diversity of morphological specializations suggest that these fishes were ecologically diverse with some being active predators capable of effective locomotion (Fig. 17). Placoderm extinction cannot be attributed to any single cause. During the Upper Devonian their decline at the Frasnian-Famennian boundary can be attributed to a global extinction event (SEPKOSKI, 1986; MCMILLAN *et al.*, 1988); however, the event did not equally affect each of the gnathostome clades present at that time. After a reduction in diversity of over 57% (table 1) there is evidence for a partial recovery among arthrodires during the Upper Famennian where they were competing with rapidly

FIG. 17. — A life reconstruction of two *Dunkleosteus terrelli* with the right individual in active pursuit of *Cladoselache* sp. Drawn by Joseph WINANS, © 1992.

Reconstitution de deux Dunkleosteus terrelli, *l'individu de droite poursuivant un* Cladoselache *sp. Dessin de Joseph* WINANS, *© 1992.*

evolving chondrichthyans and actinopterygians. The Frasnian-Famennian extinction episode, by reducing placoderm diversity, may have provided a "window of opportunity" for early radiation of chondrichthyans and actinopterygians. Placoderm evolution had centered on diverse, but limited modifications of primitive patterns of locomotion and suspensorium. The evolution of specialized actinopterygian subcarangiform and carangiform locomotion provided cost effective improvements over primitive anguilliform or modified anguilliform patterns (WEBB, 1982). Actinopterygians and chondrichthyans also demonstrated a greater plasticity in development of structural modifications for feeding. The Early Mississippian extinction of placoderms is consistent either with competitive displacement or with opportunistic replacement following the global Famennian-Tournaisian extinction event. It is possible, even likely, that both factors may play a role. Distinguishing between these two models requires a more complete understanding of early osteichthyan diversity. Due to the high reported levels of endemism among placoderms, the interrelationships among gnathostomes should be verified regionally as well.

Finally, additional study is needed to evaluate these and other hypotheses of placoderm evolution. An integrative approach considering environmental, geographic, and biological interactions with a renewed emphasis on field work will shed new light on placoderm, as well as overall gnathostome, evolution.

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TABLE 1. Species- and genus level Frasnian-Famennian extinctions (percent reduction) for substage and stage. (*) indicates an increase across the F-F boundary. The number of taxa present before and after the extinction event are recorded in parentheses.

*Pourcentages, par sous-étages et étages, des espèces et genres présents après l'extinction du Frasnien-Famennien. L'astérisque * indique une augmentation des taxons après la crise du Frasnien-Famennien. Le nombre de taxons présents avant et après l'extinction est indiqué entre paranthèses.*

Taxon	Stage spp.	Stage gen.	Substage spp.	Substage gen.
Placodermi	51% (262-128)	52% (101-48)	48% (211-110)	53% (81-38)
Antiarcha	34% (73-48)	58% (12-5)	30% (69-48)	58% (12-5)
Arthrodira	59% (148-60)	57% (67-29)	61% (104-41)	62% (47-18)
Petalichthyida	50% (2-1)	50% (2-1)	50% (2-1)	50% (2-1)
Phyllolepida	*175% (3-10)	0% (2-2)	*175% (3-10)	0% (2-2)
Ptyctodontida	77% (31-7)	71% (7-2)	75% (28-7)	71% (7-2)
Rhenanida	100% (1-0)	100% (1-0)	100% (1-0)	100% (1-0)
Aspinothoracida	43% (37-21)	25% (16-12)	71% (34-10)	56% (16-7)

APPENDIX I

Stratigraphic ranges for placoderm species compiled from DENISON (1978) and the Zoological Record (1975-1991). Range through method is employed for taxa known from disjunct stages or substages (e.g. GED-EMS or L. GED-U. GED). Taxa known from distinct stages are fully recorded (e.g. GED, SIG, EMS). Ranges with poor stratigraphic resolution are recorded to the level known (e.g. L. DEV or DEV). Taxonomy, in the most part, follows that of DENISON (1978); phlyctaeniid and actinolepid taxonomy after GOUJET (1984a) and "primitive" brachythoracids after LELIEVRE (1988). *Dinichthys herzeri* (CARR and HLAVIN, MS) along with *Gorgonichthys clarki* and *Heintzichthys gouldii* (CARR, 1991) are assigned to Aspinothoracidi *incertae sedis*. * - *Torosteus*, a *nomen nudum*, is replaced by *Goujetosteus* by Kim DENNIS-BRYAN in this volume (p. 133).

Répartitions stratigraphiques des espèces de Placodermes d'après les données de DENISON (1978) et le Zoological Record (1975-1991). Les répartitions de taxa dans des étages ou des sous-étages disjoints sont indiquées (par ex.: GED-EMS ou L. GED-U. GED). Les taxons présents dans des étages distinctes sont notés (par ex.: GED, SIG, EMS). Les répartitions stratigraphiques imprécises sont indiquées par référence au système ou sous système (par ex.: L. DEV ou DEV). La systématique utilisée suit celle de DENISON (1978); la systématique des phlyctaeniides et des actinolépides est celle de GOUJET (1984a), celle des "Brachyhtoraci primitifs" est celle de LELIÈVRE (1988). Dinichthys herzeri *(CARR & HLAVIN, MS) de même* Gorgonichthys clarki *et* Heintzichthys gouldii *(CARR, 1991) sont rapportées aux aspinothoracides* incertae sedis. * Torosteus, *considéré comme un* nomen nudum *est remplacé par le nouveau nom de genre* Goujetosteus *créé par Kim DENNIS-BRYAN dans ce volume (p. 133).*

Order STENSIOELLIDA	
Family STENSIOELLIDAE	
Stensioella heintzi	L. EMS
Order PSEUDOPETALICHTHYIDA	
Family PARAPLESIOBATIDAE	
Paraplesiobatis heinrichi	L. EMS
Pseudopetalichthys problematica	L. EMS
Order RHENANIDA	
Family ASTEROSTEIDAE	
Asterosteus stenocephalus	EIF
Asterosteus? sp.	EIF
Brollina heroldi	L. EMS
Gemuendina stuertzi	L. EMS
Jagorina pandora	U. FRS
Ohioaspis tumulosus	EIF
Ohioaspis sp.	EMS-EIF
Asterosteidae gen. et sp. indet.	GED or SIG
Family WEEJASPERASPIDIDAE	
Murrindalaspis bairdi	L. DEV
Murrindalaspis wallacei	L. DEV
RHENANIDA *incertae sedis*	
Bolivosteus chacomensis	M. DEV
Brindabellaspis stensioi	EMS
Tyriolepis radiata	L. DEV
Order PTYCTODONTIDA	
Family PTYCTODONTIDAE	
Campbellodus decipiens	L. FRS
Chelyophorus pskovensis	FRS
Chelyophorus verneuili	FAM
Chelyophorus sp.	U. DEV
Ctenurella gardineri	L. FRS
Ctenurella gladbachensis	L. FRS
Ctenurella sp.	FRS
Desmoporella minor	GIV
Eczematolepis fragilis	EIF, FRS
Eczematolepis telleri	GIV
Goniosteus gerolsteinensis	EIF
Palaeomylus crassus	EIF
Palaeomylus fragens	EIF
Palaeomylus greeni	GIV
Palaeomylus hussakofi	FRS
Palaeomylus lunaeformis	FRS
Palaeomylus minor	FRS
Palaeomylus predator	?
Palaeomylus sp.	GIV, FRS
Ptyctodopsis menzeli	GIV
Ptyctodus bradyi	FRS
Ptyctodus calceolus	GIV, FRS
Ptyctodus compressus	GIV, FRS
Ptyctodus czarnockii	FRS
Ptyctodus eastmani	FAM
Ptyctodus ferox	GIV, FRS
Ptyctodus howlandi	FRS
Ptyctodus kielcensis	FRS
Ptyctodus major	U. DEV
Ptyctodus molaris	M. DEV
Ptyctodus obliquus	FRS
Ptyctodus panderi	M. DEV
Ptyctodus punctatus	EIF
Ptyctodus reimanni	EIF
Ptyctodus sibericus	FRS

Ptyctodus sp.	EIF, GIV
Ptyctodus sp.	GIV
Rhamphodopsis threiplandi	U. EIF
Rhamphodopsis trispinatus	M. DEV
Rhynchodus excavatus	GIV
Rhynchodus eximius	U. FRS
Rhynchodus major	EIF
Rhynchodus marginalis	FRS
Rhynchodus ornatus	FRS
Rhynchodus pertenuis	FRS
Rhynchodus rostratus	GIV
Rhynchodus secans	EIF
Rhynchodus telleri	FRS
Rhynchodus tetrodon	U. FRS
Rhynchodus wildungensis	U. FRS
Rhynchodus sp.	EIF, GIV, FRS
Rhynchodus sp.	GIV
Tollodus brevispinus	SIG
PTYCTODONTIDA indeterminant	
Ptyctodontida gen. et sp. indet.	U. DEV
Ptyctodontida gen. et sp. indet.	EIF or GIV
Ptyctodontida gen. et sp. indet.	U. DEV
Ptyctodontida gen. et sp. indet.	L. or M. EIF
Ptyctodontida gen. et sp. indet.	FAM
Order ACANTHOTHORACI	
Family PALAEACANTHASPIDIDAE	
Breizosteus armoricensis	L. SIG
Dobrowlania podolica	M. GED
Kimaspis tienshanica	L. GED
Kolymaspis sibirica	L. DEV, GED?
Kosoraspis peckai	L. or M. SIG
Palaeacanthaspis vasta	M. GED
Radotina kosorensis	L. or M. SIG
Radotina prima	L. or M. SIG
Radotina tessellata	U. SIG or L. EMS
Radotina sp.	SIG
Romundina stellina	M. GED
Order PETALICHTHYIDA	
Family MACROPETALICHTHYIDAE	
Diandongpetalichthys liaojiaoshanensis	L. DEV
Ellopetalichthys scheii	GIV
Epipetalichthys wildungensis	U. FRS
Lunaspis broilii	SIG, L. EMS
Lunaspis heroldi	L. EMS
Lunaspis pruemiensis	U. EMS
Lungmenshanaspis kiangyouensis	L. DEV
Macropetalichthys agassizi	GIV
Macropetalichthys pelmensis	GIV
Macropetalichthys rapheidolabis	EIF
Notopetalichthys hillsi	U. EMS
Quasipetalichthys haikouensis	GIV-FAM
Sinopetalichthys kueiyangensis	SIG
Wijdeaspis arctica	EIF, GIV
Wijdeaspis cf. arctica	EIF
Wijdeaspis warrooensis	EMS
Wijdeaspis sp.	L. DEV, EIF
Xinanpetalichthys shendaowanensis	L. DEV
Macropetalichthyidae gen. et sp. indet.	L. DEV
Macropetalichthyidae *incertae sedis*	
Shearsbyaspis oepiki	?
Order PHYLLOLEPIDA	
Family PHYLLOLEPIDIDAE	
Austrophyllolepis ritchiei	FRS
Austrophyllolepis youngi	FRS
Phyllolepis concentrica	FAM
Phyllolepis delicatula	U. FRS
Phyllolepis konincki	FAM
Phyllolepis nielseni	FAM
Phyllolepis orvini	FAM
Phyllolepis tolli	FAM
Phyllolepis undulata	FAM
Phyllolepis woodardi	FAM
Phyllolepis sp.	FAM
Phyllolepis sp.	FAM
Placolepis budawangensis	FAM
Order ARTHRODIRA	
Family ACTINOLEPIDIDAE	
Asiacanthus kaoi	GED or SIG
Asiacanthus multituberculatus	GED or SIG
Asiacanthus suni	GED or SIG
Actinolepis magna	GIV?
Actinolepis spinosa	SIG?
Actinolepis tuberculata	EIF?
Aethaspis major	SIG
Aethaspis utahensis	SIG
Ailuracantha dorsifelis	SIG or L. EMS
Anarthraspis chamberlini	SIG
Anarthraspis montana	SIG
Baringaspis dineleyi	GED
Bollandaspis wöschmidti	EMS
Bryantolepis brachycephala	SIG
Bryantolepis cristata	SIG
Bryantolepis [Euryaspis] major	SIG
Bryantolepis sp.	SIG
Eskimaspis heintzi	GED
Heightingonaspis anglica	U. GED, L. SIG
Heightingonaspis? clarki	U. GED
Heightingonaspis? willsi	L. SIG
Kujdanowiaspis angusta	U. GED, L. SIG
Kujdanowiaspis buczacziensis	U. GED, L. SIG
Kujdanowiaspis podolica	U. GED, L. SIG
Kujdanowiaspis prominens	U. GED, L. SIG
Kujdanowiaspis rectiformis	U. GED, L. SIG
Kujdanowiaspis vomeriformis	U. GED, L. SIG
Kujdanowiaspis zychi	U. GED?, L. SIG
Lataspis brevicornis	SIG?, EMS
Lataspis rotundicornis	EMS

Lehmanosteus hyperboreus	SIG?
Mediaspis problematica	EIF
Overtonaspis billballi	L. SIG
Phlyctaenaspis extensa	U. GED, L. SIG
Proaethaspis ohioensis	L. SIG
Qataraspis deprofundis	L.DEV or EIF?
Sigaspis lepidophora	L. SIG
Simblaspis cachensis	SIG
Stuertzaspis germanica	L. EMS
Svalbardaspis polaris	EMS
Svalbardaspis rotunda	EMS
'*Svalbardaspis*' *stensioei*	SIG
Szeaspis yunnanensis	L. DEV
Szeaspis sp.	L. DEV
Wheathillaspis wickhamkingi	L. SIG

ACTINOLEPIDIDAE indeterminant

Actinolepididae indet.	GED or SIG

Family ARCTASPIDIDAE

Arctaspis hoegi	SIG
Arctaspis hoeli	SIG
Arctaspis holtedahli	SIG
Arctaspis kiaeri	SIG
Arctaspis maxima	SIG, L. EIF?
Arctaspis minor	SIG
Dicksonosteus arcticus	SIG

Family ARCTOLEPIDIDAE

Arctolepis brevis	EMS
Arctolepis decipiens	EMS
Arctolepis lata	EMS
Arctolepis lewini	EMS
Arctolepis longicornis	EMS
Arctolepis solnoerdali	EMS
Arctolepis sp	EIF
Heintzosteus brevis	SIG?
Parawilliamsaspis yujiangensis	GED? or SIG?
Arctolepididae indet.	?

Family BRACHYDEIRIDAE

Brachydeirus bicarinatus	U. FRS
Brachydeirus carinatus	U. FRS
Brachydeirus gracilis	U. FRS
Brachydeirus grandis	U. FRS
Brachydeirus loefgreeni	?
Brachydeirus magnus	U. FRS
Brachydeirus minor	U. FRS
Oxyosteus magnus	U. FRS
Oxyosteus rostratus	U. FRS
Oxyosteus sp.	M. FRS
Synquichenia coalescens	U. FRS

Family BUCHANOSTEIDAE

Buchanosteus confertituberculatus	EMS
Kueichowlepis sinensis	SIG?
Parabuchanosteus murrumbidgeensis	EMS
Buchanosteidae? gen. et sp. indet.	EIF or GIV

Family BUNGARTIIDAE

Bungartius perissus	U. FAM

Family CAMUROPISCIDAE

Camuropiscis concinnus	L. FRS
Camuropiscis laidlawi	L. FRS
Fallacosteus turneri	L. FRS
Latocamurus coulthardi	L. FRS
Rolfosteus cunningensis	L. FRS
Tubonasus lennardensis	L. FRS

Family COCCOSTEIDAE

Belgiosteus mortelmansi	GIV
Clarkeosteus halmodeus	EIF or L. GIV
Clarkeosteus sp.	GIV
Coccosteus cuspidatus	EIF
Coccosteus grossi	EIF
Coccosteus markae	GIV
Coccosteus? agassizi	?
Coccosteus? cuyahogae	FAM (U. FAM?)
Coccosteus? fritschi	?
Coccosteus? hercynius	?
Coccosteus? obtusus	?
Coccosteus? occidentalis	EIF
Coccosteus? terranovae	U. DEV
Coccosteus? sp.	L. FRS
Dickosteus threiplandi	U. EIF, L. GIV
Dickosteus sp.	EIF
Eldenosteus arizonensis	FRS
Janiosteus timanicus	FRS
Jiuchengia longoccipita	M. DEV
Millerosteus minor	L. GIV
Millerosteus orvikui	EIF
Millerosteus sp.	GIV
Millerosteus? acuminatus	EIF
Plourdosteus canadensis	L. FRS
Plourdosteus grossi	M. FRS
Plourdosteus livonicus	L. FRS
Plourdosteus mironovi	M. FRS
Plourdosteus trautscholdi	FRS
Plourdosteus sp.	GIV
Plourdosteus sp.	L. FRS
Plourdosteus sp.	FRS
Plourdosteus? magnus	L. FRS
Plourdosteus? panderi	L. FRS
Protitanichthys fossatus	EIF
Protitanichthys rockportensis	L. GIV
Protitanichthys cf. rockportensis	GIV
Watsonosteus fletti	U. GIV
Watsonosteus cf. fletti	GIV
Woodwardosteus spatulatus	EIF
Coccosteidae gen. et sp. indet.	L. or M. EIF

Super Family COCCOSTEOIDEI

Pinguosteus thulborni	L. FRS

COCCOSTEOMORPHS

Ardennosteus ubaghsi	U. FAM
Bruntonichthys multidens	L. FRS
Bullerichthys fascidens	L. FRS
Harrytoombsia elegans	L. FRS
Incisoscutum rithiei	L. FRS
Kendrickichthys cavernosus	L. FRS
Kimberia heintzi	L. FRS

Family DUNKLEOSTEIDAE [DINICHTHYIDAE]

Belosteus elegans	U. FRS
Brachyosteus dietrichi	U. FRS
Brachyosteus ooensis	FRS
Cyrtosteus inflatus	U. FRS
Dinichthys? bohemicus	EIF
Dinichthys? canadensis	GIV
Dinichthys? ceterus	L. FAM
Dinichthys? insolitus	L. FRS
Dinichthys? jeffersonensis	FRS?
Dinichthys? lincolni	U. EIF or L. GIV
Dinichthys? machlaevi	FAM
Dinichthys? oviformis	GIV
Dinichthys? pelmensis	M. DEV
Dinichthys? subgracilis	FRS
Dinichthys? tenuidens	FRS
Dunkleosteus denisoni	L. FAM
Dunkleosteus magnificus	FRS
Dunkleosteus marsaisi	L. FAM
Dunkleosteus missouriensis	U. DEV
Dunkleosteus newberryi	FRS
Dunkleosteus terrelli	U. FRS-U. FAM
Dunkleosteus yunnanensis	GIV?
Dunkleosteus n. sp. 1	FRS
Dunkleosteus n. sp. 2	U. DEV
Dunkleosteus? belgicus	FAM
Eastmanosteus calliaspis	L. FRS
Eastmanosteus egloni	FRS
Eastmanosteus licharevi	U. FRS
Eastmanosteus pustulosus	GIV, L. FRS, L. FAM
Eastmanosteus? aduncus	L. FRS
Eastmanosteus? precursor	U. EIF
Eastmanosteus? tuberculatus	L. FAM
Eastmanosteus? sp.	GIV
Golshanichthys asiatica	L. FRS
Hadrosteus rapax	U. FRS
Heintzichthys denticulatus	L. FRS
Heintzichthys dolichocephalus	M. FRS
Heintzichthys insignis	L. FRS
Heintzichthys ringuebergi	M. FRS
Heintzichthys sp.	FRS
Heintzichthys? mixeri	M. FRS
Holdenius holdeni	U. FAM
Hussakofia minor	U. FAM
Kiangyousteus yohii	GIV
Parabelosteus acuticeps	U. FRS
Parabelosteus pusillus	U. FRS
Parabelosteus tuberculatus	U. FRS
Trematosteus fontanellus	U. FRS
Westralichthys uwagedensis	M. FAM
Dinichthyidae gen. et sp. indet.	FRS

Family GEMUENDENASPIDIDAE

Gemuendenaspis angusta	L. EMS

Family GROENLANDASPIDIDAE

Groenlandaspis antarctica	U. DEV
Groenlandaspis disjectus	U. DEV
Groenlandaspis macromus	FAM
Groenlandaspis mirabilis	L. FAM
Groenlandaspis seni	FRS, FAM
Groenlandaspis sp.	U. DEV

Family HETEROSTEIDAE

Herasmius granulatus	L. EIF
Heterosteus asmussi?	EIF
Heterosteus convexus	EIF
Heterosteus eurynotus?	?
Heterosteus gracilior?	?
Heterosteus groenlandicus	L. GIV
Heterosteus hueckii?	?
Heterosteus ingens	EIF
Heterosteus initialis?	EIF
Heterosteus kutorgae?	EIF
Heterosteus rhenanus	GIV
Heterosteus secundarius?	?
Heterosteus sp.	EIF
Heterosteus sp.	GIV
Yinostius major	M. DEV

Family HOLONEMATIDAE

Artenolepis golshanii cf. Holonema	EIF, FRS
Artesonema meatsi	FRS
Belemnacanthus giganteus	M. DEV
Deirosteus abbreviatus	FRS
Deirosteus angustatus	EIF
Deirosteus omaliusi	?
Deirosteus sp.	EIF, FRS?
Deveonema obrucevi	FRS
Glyptaspis verrucosa	U. FAM
Glyptaspis sp.	FRS
Gyroplacosteus butovi	FRS
Gyroplacosteus panderi	FRS
Gyroplacosteus vialowi	FRS
Gyroplacosteus sp.	L. FRS
Holonema arcticum	L. GIV
Holonema farrowi	GIV
Holonema hatti	GIV?
Holonema harmae	GIV
Holonema horridum	FRS
Holonema obrutshevi	EIF
Holonema ornatum	GIV
Holonema radiatum	GIV, FRS
Holonema cf. radiatum	EIF, FRS
Holonema rugosum	GIV, FRS
Holonema cf. rugosum	FRS

Holonema westolli	L. FRS
Holonema sp.	EIF
Holonema sp.	GIV
Holonema sp.	FRS
Holonema sp.	U. DEV
Holonema sp.	GIV
Holonema sp.	L. or M. EIF
Holonema sp.	FAM
Megaloplax marginalis	FRS
Rhenonema eifeliense	GIV
Tropidosteus curvatus	GIV
Family Leiosteidae	
Erromenosteus brachyrostris	U. FRS
Erromenosteus concavus	U. FRS
Erromenosteus diensti	U. FRS
Erromenosteus inflatus	U. FRS
Erromenosteus koeneni	U. FRS
Erromenosteus lucifer	U. FRS
Erromenosteus platycephalus	U. FRS
Family Leptosteidae	
Leptosteus bickensis	U. FRS
Leptosteus involutus	FRS
Family Mylostomatidae	
Dinomylostoma beecheri	M. FRS
Dinomylostoma buffaloensis	L. FRS
Dinomylostoma eastmani	U. DEV
Dinomylostoma sp.	FRS
Dinomylostoma? sp.	GIV
Dinomylostoma? sp.	L. FRS
Mylostoma eurhinus	U. FAM
Mylostoma newberry	U. FAM
Mylostoma variabile	U. FAM
Tafilalichthys lavocati	L. FAM
Family Panxiosteidae	
Panxiosteus ocullus	GIV
Family Phlyctaeniidae	
Aggeraspis heintzi	U. SIG
Cartieraspis nigra	EMS or EIF
Diadsomaspis elongata	U. EMS
Diadsomaspis remscheidensis	U. EMS
Elegantaspis reticornis	SIG
Exutaspis megista	M. DEV
Gaspeaspis cassivii	EMS or EIF
Heterogaspis acuticornis	EMS
Heterogaspis borealis	EMS
Heterogaspis gigantea	EMS
Heterogaspis hornsundi	L. DEV
Heterogaspis minuta	L. DEV
Huginaspis broeggeri	EIF
Huginaspis vogti	M. DEV
Kolpuspis beaudryi	EMS or EIF
Kunmingolepis lucaowanensis	M. DEV
Laurentaspis splendida	EMS or EIF
Neophlyctaenius sherwoodi	FRS
Pageauaspis russelli	EMS or EIF
Phlyctaenius acadicus	EMS or EIF
Phlyctaenius atholi	EMS or EIF
Phlyctaenius fulgens	EMS or EIF
Phlyctaenius stenosus	EMS or EIF
Phlyctaenius? extensa	?
Phlyctaenius? major	?
Phlyctaenius? pusilla	?
Prosphymaspis constricta	L. EMS
Prosphymaspis? corneti	L. SIG
Yangaspis jinningensis	M. DEV
Phlyctaeniidae indeterminant	
Phlyctaeniidae indet.	GED or SIG
Phlyctaenaspinae indeterminant	
Phlyctaenaspinae indet.	GED? or SIG?
Phlyctaenioidea	
Barrydalaspis theroni	GIV
Phlyctaenii indet.	L. or M. EIF
Family Pholidosteidae	
Malerosteus gorizdroae	FRS
Pholidosteus bidorsatus	FRS
Pholidosteus compactus	?
Pholidosteus defectus	?
Pholidosteus friedeli	FRS
Pholidosteus laevior	FRS
Pholidosteus pygmaeus	FRS
Tapinosteus heintzi	FRS
Family Rhachiosteidae	
Rhachiosteus pterygiatus	U. GIV or L. FRS
Family Selenosteidae	
Braunosteus schmidti	U. FRS
Enseosteus hermanni	U. FRS
Enseosteus jaekeli	U. FRS
Enseosteus pachyostoides	U. FRS
Gymnotrachelus hydei	U. FAM
Melanosteus occitanus	U. FRS
Microsteus angusticeps	U. FRS
Microsteus dubius	U. FRS
Pachyosteus bulla	U. FRS, FAM
Pachyosteus grossi	U. FRS
Paramylostoma arcualis	U. FAM
Rhinosteus parvulus	U. FRS
Rhinosteus traquairi	U. FRS
Rhinosteus tuberculatus	U. FRS
Selenosteus brevis	U. FAM
Selenosteus sp.	FRS
Stenosteus glaber	U. FAM
Stenosteus pertenius	FRS?
Stenosteus sp.	FRS or L. FAM
Stenosteus sp.	L. FAM
Stenosteus n. sp. 1	U. FAM

Family TIARASPIDIDAE

Dichotiaraspis barbarae	EMS
Tiaraspis subtilis	U. SIG, L. EMS?
Tiaraspis sp.	U. DEV?
Tiaraspis sp.	EMS

Family TITANICHTHYIDAE

Titanichthys agassizi	FAM
Titanichthys attenuatus	FAM
Titanichthys clarkii	FAM
Titanichthys hussakofi	FAM
Titanichthys rectus	FAM
Titanichthys termieri	L. FAM
Titanichthys sp.	FAM
Titanichthys? kozlowskii	U. FAM

Family TOROSTEIDAE

Torosteus pulchellus*	L. FRS
Torosteus tuberculatus*	L. FRS

Family WILLIAMSASPIDIDAE

Williamsaspis bedfordi	U. EMS

Family WUTTAGOONASPIDIDAE

Wuttagoonaspis fletcheri	EIF

BRACHYTHORACI indeterminant

Maideria falipoui	L. or M. GIV
Brachythoraci gen. indet.	L. DEV

'primitive' BRACHYTHORACIDS

Arenipiscis westolli	EMS
Antineosteus lehmani	U. EMS
Atlantidosteus hollardi	U. EMS
Errolosteus goodradigbeensis	EMS
Errolosteus cf. goodradigbeensis	L. DEV
Taemasosteus maclartiensis	U. EMS
Taemasosteus novaustrocambricus	EMS

Family HOMOSTEIDAE

Angarichthys hyperboreus	U. EIF or L. GIV
Euleptaspis depressa	M.-U. SIG
'Euleptaspid A'	EMS
'Euleptaspid B'	EMS
Euleptaspididae indet.	SIG
Euleptaspididae indet.	U. EMS
Homosteus anceps	?
Homosteus arcticus	L. EIF
Homosteus cf. arcticus	EMS
Homosteus cataphractus	?
Homosteus formosissimus	EIF
Homosteus kochi	GIV
Homosteus latus	EIF
Homosteus manitobensis	EIF
Homosteus milleri	GIV
Homosteus ponderosus	?
Homosteus sulcatus	EIF
Homosteus sp.	EIF
Homosteus sp.	GIV
Luetkeichthys borealis	M. DEV
Lophostracon spitzbergense	SIG or EMS
Tityosteus orientalis	L. EMS
Tityosteus rieversi	L. EMS

PACHYOSTEOMORPHI indeterminant

Livosteus grandis	EIF, GIV, L. FRS

ASPINOTHORACIDI *incertae sedis*

Dinichthys herzeri	FRS
Gorgonichthys clarki	U. FAM
Heintzichthys gouldii	U. FAM, L. FRS?

EUBRACHYTHORACIDI *incertae sedis*

Simosteus tuberculatus	L. FRS
Ulrichosteus milesi	U. GIV

DOLICHOTHORACI indeterminant FAM

Dolichothoraci gen. et sp. indet.	FAM

ARTHRODIRA *incertae sedis*

Antarctolepis gunni	M. or U. DEV
Arctonema crassum	M. DEV?
Arctonema sp.	EIF
Aspidichthys clavatus	FRS
Aspidichthys ingens	FRS
Aspidichthys sp.	FAM
Aspidichthys sp.	U. FRS
Aspidichthys sp.	U. DEV
Aspidichthys? notabilis	M., U. DEV
Callognathus regularis	FRS, FAM
Copanognathus crassus	L. FRS
Cosmacanthus malcolmsoni	FRS or FAM
Cosmacanthus? sp.	M. or U. DEV
Diplognathus mirabilis	FAM
Grazosteus hoernesi	M. DEV?
Hollardosteus marocanus	U. GIV
Machaerognathus woodwardi	L. FRS
Murmur arcuatus	SIG
Platyaspis tenuis	FRS
Prescottaspis dineleyi	L. SIG
Taunaspis eurystethes	SIG
Timanosteus tchernychevi	FRS
Trachosteus clarki	U. FAM

Family ANTARCTASPIDIDAE

Antarctaspis mcmurdoensis	M. or U. DEV

ARTHRODIRA indeterminant

Arthrodira gen. et sp. indet.	L. DEV
Arthrodira gen. et sp. indet.	PRID
Arthrodira gen. et sp. indet.	GIV
Arthrodira? gen. et sp. indet.	WEN
Arthrodira? indet.	U. DEV

Order ANTIARCHA

Family ASTEROLEPIDIDAE (PTERICHTHYODIDAE)

Asterolepis chadwicki	FRS
Asterolepis dellei	GIV
Asterolepis estonica	EIF

Asterolepis maxima	FRS
Asterolepis orcadensis	GIV
Asterolepis ornata	L. FRS
Asterolepis radiata	L. FRS
Asterolepis saevesoederberghi	GIV
Asterolepis scabra	GIV
Asterolepis sinensis	FAM
Asterolepis thule	GIV
Asterolepis sp.	GIV
Asterolepis sp.	GIV
Asterolepis sp.	M. DEV
Asterolepis sp.	M. or U. DEV
Asterolepis sp.	FRS
Asterolepis sp.	FRS
Asterolepis sp.	GIV
Asterolepis? bohemica	?
Asterolepis? malcolmsoni	?
Asterolepis? ornata var. australis	?
Asterolepis? speciosa	?
Asterolepis? wenkenbachii	?
Byssacanthus crenulatus	EIF
Byssacanthus dilataus	EIF, GIV
Byssacanthus gosseleti	FRS
Gerdalepis dohmi	GIV, FRS
Gerdalepis jesseni	M. EIF
Gerdalepis luedenscheidensis	?
Gerdalepis rhenana	EIF, GIV
Pterichthyodes milleri	M. DEV
Pterichthyodes productus	M. DEV
Pterichthyodes cf. P. sp.	EMS
Pterichthyodes? cellulosus	?
Pterichthyodes? elegans	?
Pterichthyodes? harderi	?
Pterichthyodes? striatus	?
Remigolepis acuta	FAM or L. CARB
Remigolepis cristata	FAM or L. CARB
Remigolepis incisa	FAM or L. CARB
Remigolepis kochi	FAM or L. CARB
Remigolepis kullingi	FAM or L. CARB
Remigolepis major	FAM
Remigolepis microcephala	FAM
Remigolepis xiangshanensis	FAM
Remigolepis xixiaensis	FAM
Remigolepis zhongningensis	FAM
Remigolepis zhongweiensis	FAM
Remigolepis sp.	FRS
Remigolepis sp.	TOU
Remigolepis? tuberculata	FAM or L. CARB
Stegolepis asiatica	FRS
Stegolepis jugata	FRS
Wurungulepis denisoni	M. DEV
Hyrcanaspis bliecki	EIF

Suborder ASTEROLEPIDOIDEI

Pambulaspis cobandrahensis	?
Pambulaspis antarctica	GIV, FRS
Sherbonaspis hillsi	EIF
Asterolepidoid indet.	EMS

Family BOTHRIOLEPIDIDAE

Bothriolepis alexi	GIV, FRS
Bothriolepis alvesiensis	FAM
Bothriolepis amankonyrica	FRS
Bothriolepis antarctica	M. or U. DEV
Bothriolepis askini	GIV, FRS
Bothriolepis barretti	GIV, FRS
Bothriolepis bindarvei	FRS
Bothriolepis canadensis	FRS
Bothriolepis cellulosa	FRS
Bothriolepis ciecere	FAM
Bothriolepis coloradensis	FRS
Bothriolepis cristata	FAM
Bothriolepis cullodenensis	FRS
Bothriolepis curonica	FRS
Bothriolepis darbiensis	FAM?
Bothriolepis evaldi	?
Bothriolepis favosa	FRS
Bothriolepis fergusoni	FRS
Bothriolepis gigantea	FAM
Bothriolepis gippslandiensis	FRS
Bothriolepis groenlandica	FAM
Bothriolepis hayi	U. DEV
Bothriolepis hickingi	U. DEV
Bothriolepis hydrophila	FAM
Bothriolepis jani	?
Bothriolepis jarviki	FAM
Bothriolepis jeremijevi	U. DEV
Bothriolepis karawaka	GIV, FRS
Bothriolepis kassini	FRS
Bothriolepis kohni	GIV, FRS
Bothriolepis kwangtungensis	GIV
Bothriolepis cf. kwangtungensis	L. or M. EIF
Bothriolepis laverocklochensis	FAM
Bothriolepis leptocheira	U. DEV
Bothriolepis lochangensis	GIV
Bothriolepis lohesti	FAM
Bothriolepis macphersoni	GIV, FRS
Bothriolepis macrocephala	U. DEV
Bothriolepis maeandrina	U. DEV
Bothriolepis major	FRS
Bothriolepis mawsoni	GIV, FRS
Bothriolepis maxima	FRS
Bothriolepis minor	FRS, FAM
Bothriolepis nielseni	FAM or L. CARB?
Bothriolepis nikitinae	FRS
Bothriolepis nitida	U. DEV
Bothriolepis niushoushanensis	GIV-FAM
Bothriolepis obesa	U. DEV
Bothriolepis obrutschewi	FRS
Bothriolepis ornata	FAM
Bothriolepis panderi	?
Bothriolepis paradoxa	FAM
Bothriolepis pavariensis	FAM
Bothriolepis portalensis	GIV, FRS
Bothriolepis prima	FRS
Bothriolepis shuokuanensis	GIV
Bothriolepis siberica	FRS

Bothriolepis sinensis	GIV
Bothriolepis stevensoni	U. DEV
Bothriolepis tastenica	FRS
Bothriolepis tatongensis	U. GIV or L. FRS
Bothriolepis taylori	FRS
Bothriolepis traquairi	FRS
Bothriolepis tungseni	GIV
Bothriolepis turanica	FRS
Bothriolepis virginiensis	?
Bothriolepis vuwae	GIV, FRS
Bothriolepis wilsoni	U. DEV
Bothriolepis yunnanensis	GIV
Bothriolepis zadonica	?
Bothriolepis sp.	FRS
Bothriolepis sp	FRS
Bothriolepis sp.	FRS
Bothriolepis sp.	FRS
Bothriolepis sp.	FRS
Bothriolepis sp.	L. FRS
Bothriolepis sp.	FAM
Bothriolepis sp.	FAM
Briagalepis warreni	FRS
Dianolepis liui	M. DEV
Grossilepis brandi	FRS
Grossilepis spinosa	FRS
Grossilepis tuberculata	FRS (U. DEV?)
Monarolepis verrucosa	?
Vietnamaspis trii	GIV, FRS
Wudinolepis weni	M. DEV
Xichonolepis quijingensis	GIV

BOTHRIOLEPIDOIDEI

Nawagiaspis wadeae	GIV

Family CHUCHINOLEPIDIDAE

Chuchinolepis dongmoensis	?
Chuchinolepis gracilis	?

Family LIUJIANGOLEPIDIDAE

Liujiangolepis suni	GED or SIG

Family MICROBRACHIIDAE

Microbrachium sp. indet.	?
Microbrachius dicki	U. GIV
Microbrachius sinensis	GIV
Microbrachius stegmanni	?
Microbrachius sp.	U. GIV

Family PROCONDYLOLEPIDIDAE

Procondylolepis quijingensis	GED or SIG

Family QUIJINOLEPIDIDAE

Quijinolepis gracilis	L. DEV
Quijinolepis? sp.	L. DEV

Family SINOLEPIDIDAE

Sinolepis macrocephala	FAM
Sinolepis szei	FAM
Sinolepis wutungensis	FAM
Vanchienolepis langsonensis	?

Family WUDINOLEPIDIDAE

Hohsienolepis hsintuensis	M. DEV

Family YUNNANOLEPIDIDAE

Phymolepis cuifengshanensis	L. DEV
Yunnanolepis bacboensis	?
Yunnanolepis chii	L. DEV?
Yunnanolepis departi	?
Yunnanolepis parvus	L. DEV

PTERICHTHYODOIDEA

Wurungulepis denisoni	EIF

ANTIARCHA *incertae sedis*

Eoantiarchilepis xitunensis	L. DEV
Grossaspis carinata	GIV
Hillsaspis gippslandiensis	U. DEV
Hunanolepis tleni	GIV
Lepadolepis stensioei	U. FRS
Lianhuashanolepis liukiangensis	L. DEV
Orientolepis neokwangsiensis	GED or SIG
Taeniolepis speciosa	FRS
Tsuifengshanolepis diantungensis	L. DEV
Zhanjilepis aspratilis	L. DEV

ANTIARCHA indeterminant

Antiarcha indet.	L. or M. EIF
Antiarcha indet.	LUD

PLACODERMI *incertae sedis*

Changyonophyton hupeiense	U. DEV
Deinodus bennetti	EIF
Hybosteus mirabilis	U. GIV
Neopetalichthys yenmenpaensis	L. DEV
Nessariostoma granulosum	L. EMS
Oestophorus lilleyi	GIV, FRS
Sedowichthys terraboreae	M. DEV
Tollichthys polaris	M. DEV
Yunnanacanthus cuifengshanensis	DEV

PLACODERMI indeterminant
(recorded from unique localities)

Placodermi indet.	GED
Placodermi indet.	WEN
Placodermi indet.	EIF
Placodermi indet.	M. GIV-E. or L. FRS

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Some comments on the Placoderm parasphenoid

by Kim DENNIS-BRYAN

Abstract. — Parasphenoids have or are being described in thirty-nine genera of the Placodermi. All but three of the genera are arthrodires. The actual number of parasphenoids preserved is very small. A review of the literature reveals that many questions regarding this bone remain unanswered e.g. its origin, what is the primitive and advanced condition, what changes occur during growth? Though used by some authors as a character that is diagnostic of particular groups of arthrodire, it seems on existing evidence that the parasphenoid is species specific. There are few indications, at the present time, that the bone is useful in working out placoderm relationships.

Keywords. — Placodermi, parasphenoid.

Remarques sur le parashénoïde des Placodermes

Résumé. — Le parasphénoïde est connu chez trente-neuf genres de Placodermes, parmi ceux-ci trois ne sont pas des Arthrodires. Ainsi le nombre de genres où le parasphénoïde est connu est-il très restreint. Une analyse des ouvrages où cet os dermique a été décrit, révèle que bon nombre de questions reste en suspens, ainsi son origine; quels sont les états primitifs et dérivés des caractères que l'on peut définir ? Quels sont les changements qui l'affectent pendant la croissance ? Bien que des auteurs aient utilisé le parasphénoïde dans la définition de certains groupes d'Arthrodires, il semble n'être seulement caractéristique qu'au niveau spécifique. Aujourd'hui, seuls quelques traits apparaissent utiles dans l'analyse des relations de parenté des Placodermes.

Mots-clés. — Placodermes, parasphénoïde.

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INTRODUCTION

Among placoderms the parasphenoid is preserved in only a few arthrodires, the acanthothoracid *Kosoraspis*, the phyllolepid *Austrophyllolepis* and an undescribed *Bothriolepis* from Gogo, Western Australia (table 1). In most cases only the ventral surface is known. The Gogo arthrodires have provided a number of complete parasphenoids, but the significance of this bone in working out relationships remains uncertain.

BM(NH) Natural History Museum, London, United Kingdom.
WAM The Western Australian Museum, Perth, Australia.

HISTORICAL BACKGROUND

Placoderm fossils have been recognized for over a century (MCCOY, 1848), but the parasphenoid was unknown until 1936 when Edwin Sherborn HILLS, in describing the skull roof of

Buchanosteus (Coccosteus) osseus, also provided the first description of a placoderm parasphenoid. According to YOUNG (1979), the specimen described by HILLS is 'now in a poor state of repair.' However, his figures 4 and 5 show the bone to have a denticulated ventral surface and a paired buccohypophysial foramen with an incomplete ventral transverse groove posterior to it. The restored bone is shown as being longer than it is broad. WHITE & TOOMBS (1972) described three further parasphenoids of *Buchanosteus.* They too are denticulated but in these specimens the buccohypophysial foramen is sited in the ventral transverse groove. Furthermore, WHITE & TOOMBS describe the bone as 'broadly spade-shaped, about as long as wide'. YOUNG (1979) described another three parasphenoids making a total of seven. These specimens show an increase in breadth with increasing size which YOUNG interprets as an allometric growth feature.

In 1942, STENSIÖ described the parasphenoid of the actinolepid *Kujdanowiaspis* (Fig. 1A). As in *Buchanosteus,* the dorsal surface is unknown. The ventral surface is entirely covered with tubercles and is perforated by a large, undivided median buccohypophysial foramen. The outline of the bone is uncertain as there is considerable variation between STENSIÖ's (1963) figures 10A and 14. There are also differences in the shape of the buccohypophysial foramen and its spatial relationship with the foramina for the hypophysial vein.

It is in the addendum to STENSIÖ's 1945 paper on the cranium and cervical joint of the Dolichothoraci that the parasphenoid of eubrachythoracid arthrodires is first mentioned. STENSIÖ states that the bone is preserved in three genera – *Erromenosteus* (Fig. 2E), *Trematosteus* (Fig. 2F) and *Brachyosteus* – from Wildungen in Germany. There are no descriptions, only the comment that it is a 'powerful bone' extending backwards, as it does in crossopterygians and palaeonisciforms, to the transitional part between the orbito-temporal and otic regions of the endocranium.

Two eubrachythoracid parasphenoids were briefly described the following year by DUNKLE & BUNGART (1946). However, the authors considered the bone to be homologous with the anterior basal element of acanthodians and so it is labelled as such in their drawings (*Ab,* DUNKLE & BUNGART, 1946, Fig. 3). Among eubrachythoracid arthrodires there are a number of subdivisions, two of which have been adopted here (coccosteomorph and pachyosteomorph, see table 1). Both of the arthrodires described here are considered to be pachyosteomorph (for characters, see CARR, 1991). The parasphenoid of *Dunkleosteus (Dinichthys) terrelli* (Fig. 3A) is described as being 'thickened anteromesially' and with two overlap areas on its anterior margin for the posterior processes of the left and right anterior superognathals. In contrast the parasphenoid of *Heintzichthys gouldii* is said to be 'a proportionally much narrower, thin lamina of bone, strongly arched dorsally' that has no contact with the toothplates. A more detailed account of the former is mentioned by the authors to be forthcoming but has not been traced. The latter was redescribed by CARR in 1991.

JARVIK (1954) did not describe any arthrodire parasphenoids. However, in his discussion of the evolution of the parasphenoid in fishes he concluded that, in arthrodires, 'it is a thin tooth-bearing plate attached to the median parts of the ventral faces of the ethmoidal and orbito-temporal regions of the neurocranium, but is of varying shape and size and it may extend behind the ventral opening of the fossa hypophyseos, thus being pierced by a hypophysial canal, or end in front of that opening.' He considered the arthrodire parasphenoid primitive and characterized by disintergration and reduction.

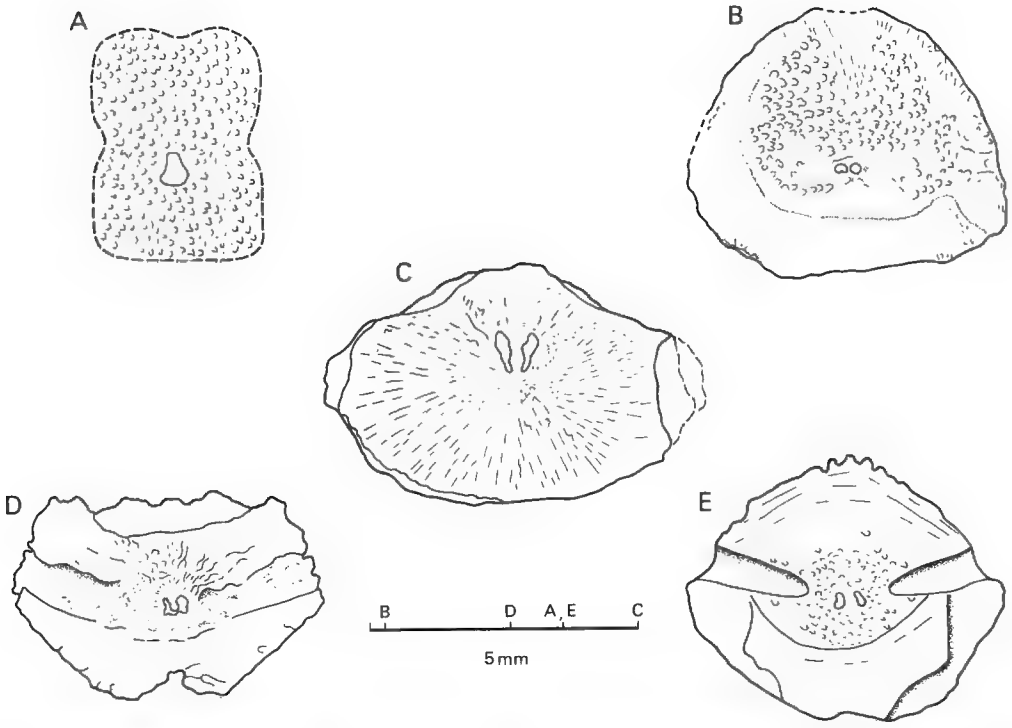

FIG. 1. — Parasphenoids in ventral view. A, *Kujdanowiaspis* sp. (from STENSIÖ, 1963, Fig. 10A). B, *Antineosteus lehmani* (from LELIÈVRE, 1988, Fig. 2A). C, *Arctolepis decipiens* (from GOUJET, 1984, Fig. 81). D, *Harrytoombsia elegans* (from MILES & DENNIS, 1979, Fig. 13A). E, *Coccosteus cuspidatus* (from MILES & WESTOLL, 1968, Fig. 18a).

Parasphénoïdes en vue ventrale. A, Kujdanowiaspis *sp. (d'après* STENSIÖ, *1963, fig. 10A). B,* Antineosteus lehmani *(d'après* LELIÈVRE, *1988, fig. 2A). C,* Arctolepis decipiens *(d'après* GOUJET, *1984, fig. 81). D,* Harrytoombsia elegans *(d'après* MILES & DENNIS, *1979, fig. 13A). E,* Coccosteus cuspidatus *(d'après* MILES & WESTOLL, *1968, fig. 18a).*

Much of the above has already been summarized by KULCZYCKI (1956). It was he who, in addition to providing the first detailed description of the eubrachythoracid parasphenoid, also divided the bone into anterior (prehypophysial) and posterior (posthypophysial) divisions. The three parasphenoids he described are referred to *Dinichthys* cf. *pustulosus, Malerosteus gorizdroae* (KULCZYCKI, 1957), and brachythoracid indet. (Fig. 3E). It is interesting to note that in the latter case the bone margin has been restored (KULCZYCKI, 1956, Pl. 1H) with the same 'feathered edge' as is seen in *Heintzichthys* (CARR, 1991, Fig. 8A).

KULCZYCKI also considered the origin of the placoderm parasphenoid. He claimed that it was a dermal bone on evidence of its histological structure and the presence of ornamentation on the ventral surface. He rejected the suggested homology (DUNKLE & BUNGART, 1946) with the anterior-basal element of acanthodians because of its perichondral origin and the absence of foramina and grooves for the internal carotids on the ventral surface.

In 1957, KULCZYCKI also described the parasphenoid of the pachyosteomorph *Pachyosteus bulla* (Fig. 3B). He considered it more primitive than those he had described previously despite

the lack of ornamentation on the ventral surface. His account of the bone is as follows: '25 mm in length and 14mm in maximum width. Its smooth and plane ventral surface has the outline of a somewhat elongate and rounded hexagon. Anteriorly it is provided with a process whose lateral margins first run parallel and then converge at a nearly right angle. Dorsally, in the hind part of the parasphenoid is a raised area with an extensive bowl-like, pituitary depression. On both lateral sides the margin of the depression is particularly raised. To the front of this depression, on its outer embankment extends a transverse groove whose lateral ends are directed arcuately backward. Medially this groove branches off into an unpaired ramification directed straight forward, along the central line, over the dorsal surface of the anterior process, which is here somewhat raised. These grooves probably contained internal carotids fusing here into one unpaired canal entering the cranial cavity.'

There were now seven descriptions of different arthrodire parasphenoids [and mention by STENSIÖ (1945) of at least three more]. It therefore seemed reasonable for KULCZYCKI (1957: 346) to assume that eventually the diversity in shape and structure of the arthrodire parasphenoid would provide...'additional evidence for the differentiation of separate evolutionary lines within this stock.'

The parasphenoid of *Kiangyousteus* (LIU, 1955) is omitted from KULCZYCKI's discussion possibly because it had been misidentified by LIU as a pineal plate. The bone is incomplete but can be seen to have the more complex structure of the previously mentioned eubrachythoracid arthrodires. It has a prehypophysial region and a thickened posterior part that houses the buccohypophysial depression and paired foramen. Using four characters, three of which refer to the unusual form of the 'pineal', LIU concluded that *Kiangyousteus* was related to the ancestral form of either *Titanichthys* or *Dinichthys*. DENISON (1978) supported the latter relationship and designated the genus to his family Dinichthyidae based in part on the similarity of the parasphenoid (and the anterior lateral) with that of *Dunkleosteus*.

LEHMAN (1956: 38-54) discusses some incomplete parasphenoids in his account of arthrodires from the Upper Devonian of Tafilalet. 'Only the central part of the parasphenoid can be observed in my material. of a *Dunkleosteus* indeterminable at the species level; the preparation of this central part shows that the dorsal face of the parasphenoid plate was excavated and in part occupied by a hypophysial fossa; at its lowest point it is pierced by two canals that open in closer proximity to one another on the lower face of the bone...'

'I add to this description two photographs of parasphenoids of american brachythoracids from the Natural History Museum attributed respectively to *Titanichthys* (P9384) and *?Protitanichthys fossatus* (P9368). These pieces seem to be generically indeterminable; it is not likely that we are dealing with *Titanichthys* for which the parasphenoid must have been larger than in the Dinichthyidae. These pieces are nonetheless interesting as examples of parasphenoids of large Brachythoraci.'

'The parasphenoids each comprise an anterior and a posterior part; the two parts being separated from one another by two symmetrical notches at the lateral edges of the bone situated level to the centre of radiation; near to the radiation centre there opens one (?) or two canals. The anterior border of the bone shows two concavities in which the anterior superognathals inserted. At either side of these concavities towards the edges of the bone, the parasphenoid has very thin expansions. The posterior border of the bone is transversely truncated between two lobes, one to the right and one to the left.'

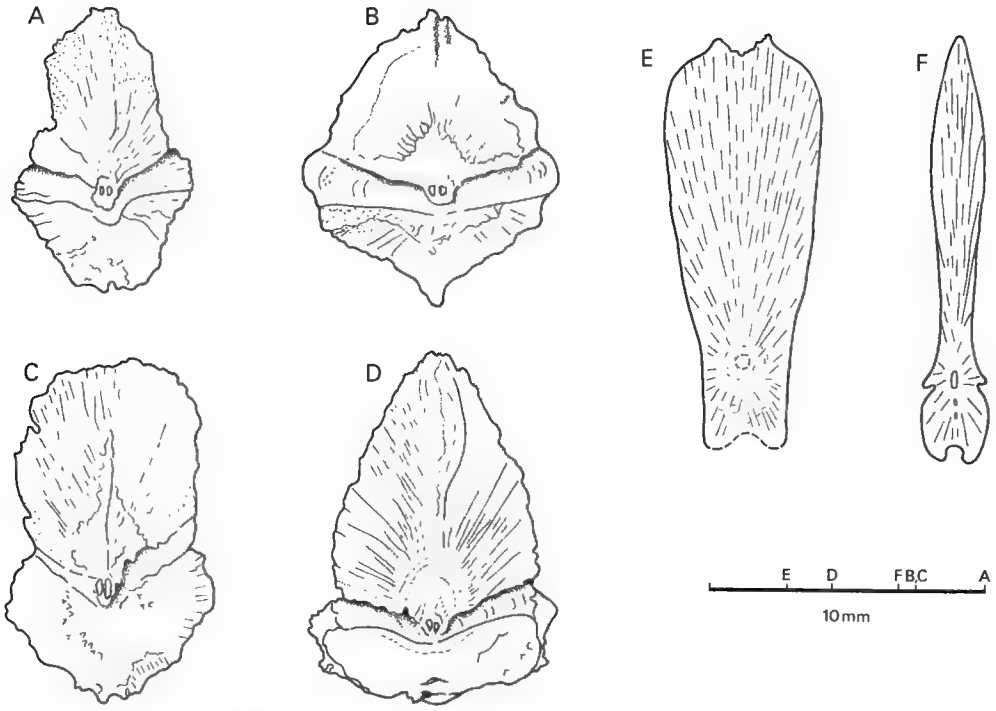

FIG. 2. — Parasphenoids in ventral view. A, *Gogopiscis gracilis* (from GARDINER & MILES, 1994, Fig. 17B). B, *Goujetosteus (Torosteus) pulchellus* (from GARDINER & MILES, 1990, Fig. 24A). C, *Bullerichthys facsidens* (from DENNIS & MILES, 1980, Fig. 9B). D, *Eastmanosteus calliaspis* (from DENNIS-BRYAN,1987, Fig. 17B). E, *Erromenosteus lucifer* (from STENSIÖ, 1963, Fig. 115E). F, *Trematosteus fontanellus* (from STENSIÖ, 1963, Fig. 92A).

Parasphénoïdes en vue ventrale. A, Gogopiscis gracilis d'après *GARDINER & MILES, 1994, fig. 17B).* B, Goujetosteus (Torosteus) pulchellus *(d'après GARDINER & MILES, 1990, fig. 24A).* C, Bullerichthys facsidens *(d'après DENNIS & MILES, 1980, fig. 9B).* D, Eastmanosteus calliaspis *(d'après DENNIS-BRYAN, 1987, fig. 17B).* E, Erromenosteus lucifer *(d'après STENSIÖ, 1963, fig. 115E).* F, Trematosteus fontanellus *(d'après STENSIÖ, 1963, fig. 92A).*

In addition it should be noted that the parasphenoid of P9368 has the same 'feathered edge' as that described by CARR (1991) for *Heintzichthys* but has a posterior configuration similar to that of *Dunkleosteus*. The so-called 'anterior concavities' for overlap with the anterior superognathals are unclear in this specimen compared with P9384. The parasphenoid of P9384 is also less robust than in P9368.

In 1959 GROSS described a non-arthrodiran parasphenoid – that of the acanthothoracid *Kosoraspis*. It most closely resembles the parasphenoid of *Kujdanowiaspis* in having a simple structure with a denticulated ventral surface bearing a single buccohypophysial foramen. However, in contrast to *Kujdanowiaspis*, the parasphenoid of *Kosoraspis* is long and narrow. The anterior margin is unclear on the figured specimen.

Another review of arthrodire parasphenoids appeared in 1963 with the publication of STENSIÖ's authoritative work on the arthrodire head. He included descriptions of four new parasphenoids and mentioned the existence of a fifth, that of the trematosteid *Brachyosteus*. STENSIÖ

divided the parasphenoids of the pachyosteomorph arthrodires into five types: trematosteid, erromenosteid, dunkleosteid, heintzichthyoid and pachyosteoid.

The trematosteid type of parasphenoid is long and narrow and has a conspicuous downward bend in its mid-region. The parasphenoids of both *Trematosteus* (Fig. 2F) and *Brachyosteus* are said to be of this type but only that of the former is described and only the ventral surface is known. The prehypophysial region is 'very long and stretches forwards between the vomers' (anterior superognathals). STENSIÖ postulates that the bones were in contact with one another but there are no overlap areas for the toothplates on the parasphenoid as there are in *Dunkleosteus*. The buccohypophysial foramen is unpaired and there is no ventral transverse groove or ornamentation.

The erromanosteid type is known only in *Erromenosteus* (Fig. 2E). It is similar to the trematosteid type in all the above features bar one, it lacks a buccohypophysial foramen. However, according to STENSIÖ it is 'very likely pierced by an unpaired buccohypophysial foramen.'.

These two types of parasphenoid along with the pachyosteoid type, which is known only by that described for *Pachyosteus* by KULCZYCKI (1957), are suggested by STENSIÖ to be characteristic of the families Trematosteidae, Leiosteidae and Pachyosteidae respectively. For example, he says of the pachyosteoid parasphenoid that 'there is strong reason to believe that a parasphenoid of this type also existed in *Enseosteus*, *Ottonosteus*, *Walterosteus* and *Parawalterosteus*.' However, this inference is made without any direct evidence that this is the case. It therefore seems equally reasonable to assume that the parasphenoids described are species specific and not as stated by Stensiö until further material becomes available for study.

The dunkleosteid and heintzichthyoid types of parasphenoid are, according to STENSIÖ, represented respectively only by the genera *Dunkleosteus* (Fig. 3A) and *Heinzichthys* both of which have already been mentioned. It should, however, be noted that *Heintzichthys*, having been cited as a pachyosteomorph arthrodire with a characteristic type of parasphenoid, is omitted from STENSIÖ's (1963: 387) familial listing of the group because, at that time, it was 'so slightly known'.

The parasphenoids of *Pholidosteus* and *Tapinosteus* are also described by STENSIÖ. That of *Pholidosteus* is long and narrow and is without notches, foramina or grooves. It is known only from the ventral surface which is covered with small tubercles. The parasphenoid of *Tapinosteus* (STENSIÖ, 1963, Fig. 71A) is of similar length, but is expanded laterally in the midregion. Again only the ventral surface is known. In contrast to *Pholidosteus*, the *Tapinosteus* parasphenoid lacks ornament and is pierced by a paired buccohypophysial foramen. At either side of the foramen there is a short transverse groove that ends in a foramen presumably for a branch of the internal carotid artery. Posteriorly there is another unpaired foramen for the median hypophysial vein. Neither parasphenoid extends far enough anteriorly to overlap with the toothplates. Despite the very different form of the parasphenoid in these two genera, they are both considered to be members of the family Pholidosteidae. As I have not been able to examine this material, I am unable to comment further.

In 1968, MILES & WESTOLL described the parasphenoid of *Coccosteus cuspidatus* (Fig. 1E). The bone is roughly circular in shape with a flat ventral surface. There is a transverse groove which is discontinuous and fades out medially at either side well short of the central region. Tubercles are restricted to this central region which is pierced by a paired buccohypophysial

foramen. The median septum that divides the foramen also divides the ill-defined buccohypophysial depression in half. Posteriorly there is a foramen for the median hypophysial vein. The posterior groove recorded by MILES & WESTOLL is re-assessed by GARDINER & MILES (1990) as 'no more than a step in the bone surface.'

In 1975, another non-brachythoracid parasphenoid, that of the phlyctaeniid *Dicksonosteus arcticus*, was described by GOUJET as a 'short tuberculated' bone with a single buccohypophysial foramen at its centre He redescribed the bone in 1984 together with those of two other phlyctaeniids, *Arctolepis decipiens* (Fig. 1C) and *Heintzosteus brevis* (GOUJET, 1984, Figs. 91, 98), and the actinolepid *Lehmanosteus hyperboreus* (GOUJET, 1984, Fig. 107). The three phlyctaeniid parasphenoids are similar in being broader than they are long, and in having reduced prehypophysial regions and anteriorly situated buccohypophysial foramina (revised by GOUJET for *D. arcticus)*. All have denticulated ventral surfaces. In contrast, in *D. arcticus* and *H. brevis* the buccohypophysial foramen is undivided whereas in *A. decipiens* it is a paired structure similar to that of certain brachythoracid arthrodires. Transverse sections of the parasphenoid in *D. arcticus* suggest a bone of mixed origin as 'the edges of the bone merge into the perichondral bone enveloping the endocranium' but 'there is also fusion between the dermal bone and the internal perichondral bone covering the hypophysial fossa.'

The parasphenoid of the actinolepid *L. hyperboreus* is most closely similar to that described by STENSIO for *Kujdanowiaspis* in that the ventral surface is featureless except for the ornament and a single buccohypophysial foramen at its centre. In shape, however, it is more like the above phlyctaeniids in that it is broader than it is long.

WANG (1979) figures the anterior ventral part of a parasphenoid in his account of *Panxiosteus occullus*. He describes the bone as being without either a hypophysial foramen or surface ornamentation but there does appear to be a transverse ventral groove. His figure 2 shows the parasphenoid with a substantial overlap for the anterior superognathals. However, it is possible that the bone has been displaced forwards thereby suggesting an unusually large overlap area. WANG concludes that 'the structure and form of the parasphenoid are similar to that of *Dinichthys*– but is distinguished [from it] by such as the central not bordering on the margin and the dermal plate with tubercles.' WANG also writes that *P. occullus* is very similar to *Pholidosteus* except for the parasphenoid in which it differs 'distinctly.'

Between 1979 and 1994, MILES, DENNIS-BRYAN (also see DENNIS), and GARDINER described parasphenoids from ten different genera of athrodire *i.e. Harrytoombsia* (Fig. 1D; MILES & DENNIS, 1979), *Bruntonichthys* (Fig. 3G) and *Bullerichthys* (Fig. 2C; DENNIS & MILES, 1980), *Incisoscutum* (DENNIS & MILES, 1981), *Simosteus* (DENNIS & MILES, 1982), *Kimberleyichthys* (DENNIS-BRYAN & MILES, 1983), *Eastmanosteus* (Fig. 2D; DENNIS-BRYAN, 1987), *Goujetosteus* (*Torosteus*) (Fig. 2B; GARDINER & MILES, 1990; VEZINA, in press) and *Compagopiscis* and Gogopiscis (Fig. 2A; GARDINER & MILES, 1994). In all, except *Bruntonichthys*, the bone is detached from the endocranium and can be viewed from both dorsal and ventral aspects. Each parasphenoid is species specific though they do have certain features in common. These similarities represent a retention of primitive features rather than the presence of shared derived features. For example, in none of the Gogo arthrodires does the parasphenoid overlap the toothplates; all have a paired buccohypophysial foramen. Only in *Eastmanosteus calliaspis* are there

a number of parasphenoids preserved and some variation in the bone has been noted e.g., the ventral groove is roofed over laterally in two of the eleven specimens.

Two other parasphenoids from Gogo arthrodires have been described by LONG (1988a, b) for the camuropiscids *Tubonasus* (Fig. 3C) and *Latocamurus* (Fig. 3D). Both bones are long and rather narrow, a feature that LONG suggests may be characteristic of the family Camuropiscididae. However, the parasphenoid is not yet known in the camuropiscid *Camuropiscis* (DENNIS & MILES, 1979a), and it is also elongated in *Bruntonichthys* which is not a member of the that family. LONG (1988a) suggests that the similarity in the *Bruntonichthys* parasphenoid is due to convergent evolution. LONG (in litt.) has also described the parasphenoid of a plourdosteid arthrodire (WAM 86.9.676) from Gogo. Its basic structure is much like that of other arthrodires from that locality.

In 1984, LONG described the parasphenoids of two phyllolepids, *Austrophyllolepis ritchiei* and *Austrophyllolepis youngi*, though only that of *A. ritchiei* is illustrated in any detail. Both appear to be very similar in structure for LONG does not distinguish between them. The ventral surface has a tuberculated central region in which there lies a paired buccohypophysial foramen.

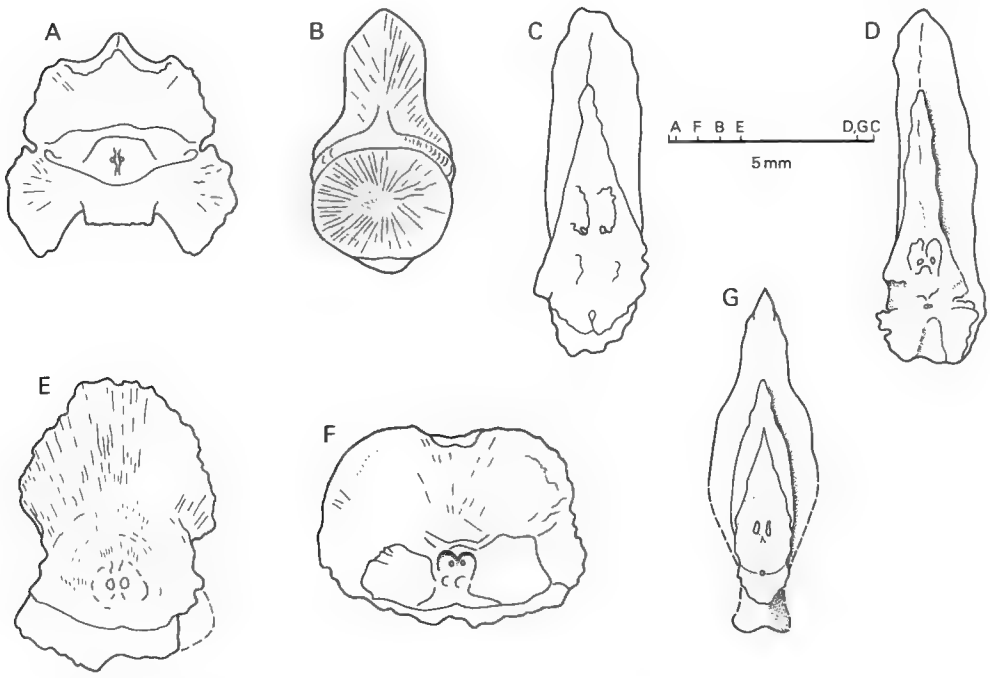

FIG. 3. — Parasphenoids in dorsal view. A, *Dunkleosteus (Dinichthys) terrelli* (from DUNKLE & BUNGART, 1946, Fig. 3A). B, *Pachyosteus bulla* (from KULCZICKI, 1957, Fig 13A). C, *Tubonasus lennardensis* (from LONG, 1988, Fig. 3B reversed). D, *Latocamurus coulthardi* (from LONG, 1988, Fig. 11B). E, Brachythoracid indet. (from KULCZYCKI, 1956, Pl. 1H). F, *Tafilalichthys lavocati* (from LELIÈVRE, 1991, Fig. 4B). G, *Bruntonichthys multidens* (from DENNIS & MILES, 1980, Fig. 3C).

Parasphénoïdes en vue dorsale. A, Dunkleosteus (Dinichthys) terrelli *(d'après* DUNKLE & BUNGART, *1946, fig. 3A). B,* Pachyosteus bulla *(d'après* KULCZICKI, *1957, fig. 13A). C,* Tubonasus lennardensis *(d'après* LONG, *1988, fig. 3B inversée). D,* Latocamurus coulthardi *(d'après* LONG, *1988, fig 11B). E, Brachythoracid indet. (d'après* KULCZYCKI, *1956, pl. 1H). F,* Tafilalichthys lavocati *(d'après* LELIÈVRE, *1991, fig. 4B). G,* Bruntonichthys multidens *(d'après* DENNIS & MILES, *1980, fig. 3C).*

The surrounding area which is only seen in the larger specimens (mature individuals) is 'incised with radial striae.' The absence of this outer region in juveniles suggests that, for this group at least, the growth of the parasphenoid is not by enlargement of the whole structure, but by addition to the periphery (LONG, 1984, Figs. 5, 6) The ventral groove is only evident at the lateral margins of the ventral surface, as it is in *Coccosteus cuspidatus*, but in shape the parasphenoid of a mature individual is most similar to that of *Buchanosteus*. The bone is situated in the centre of the head in a more posterior position than in other placoderms.

The first description of the homosteid arthrodire, *Antineosteus lehmani* (LELIÈVRE, 1984), was confined to head and trunk armour plates. However, a further publication by LELIÈVRE (1988: 289-290) describes an isolated parasphenoid, associated with typical *Antineosteus* dermal bones, showing both dorsal and ventral surfaces. The dorsal surface has a broad transverse depression at the centre of which there is a clearly divided hypophysial fossa. The ventral surface (Fig. 1B) has a large tuberculated area and is perforated by a paired buccohypophysial foramen. The general shape of the parasphenoid and the extent of the ornamented region is, according to LELIÈVRE, unique to this arthrodire and probably also to 'primitive brachythoracids' (see table 1).

In 1987 LELIÈVRE *et al.* described the parasphenoid of a selenosteid, *Melanosteus occitanus*. It has a very long, narrow prehypophysial process which has a groove of unknown function running along its dorsal surface. There is a paired hypophysial foramen on the main body of the dorsal surface but, having merged within the bone, it opens on the ventral side as a single opening. Again the form of the parasphenoid is characteristic of the brachythoracid arthrodire in which it occurs.

The parasphenoid of the type specimen of *Tafilalichthys lavocati* was described by LELIÈVRE in 1991. Both dorsal (Fig. 3F) and ventral aspects of the bone are preserved. It is rounded in shape with a paired buccohypophysial foramen. The ventral surface has a transverse ventral groove but lacks ornamentation. The dorsal surface shows moderate development of the posterolateral processes.

The parasphenoid of *Bothriolepis* sp. is currently being described by YOUNG, LONG, GARDINER and DENNIS-BRYAN. The description is based on a single example of the bone (BM(NH) P50898) from Gogo, Western Australia. There is a well developed but narrow prehypophysial process below which is an expanded region with a convex posterior margin. The lateral edges are notched as in some arthrodires but there is no buccohypophysial depression or foramen.

Other placoderms with parasphenoids preserved that are currently being described include: *Gymnotrachelus* by CARR and two species of *Dunkleosteus* also by CARR (pers. comm)

DISCUSSION

There are now many varied accounts of the parasphenoid in placoderms. Thirty-six genera are represented of which all but three are arthrodires. Despite this fairly extensive range of material, the number of parasphenoids on which the descriptions are based is small with perhaps only one or two of the bones being preserved for each species e.g. *Harrytoombsia* (1), *Tubonasus* (1), *Melanosteus* (1), *Antineosteus* (1). As a result of this, apart from a description, information

about the placoderm parasphenoid is somewhat limited. Origin, variations, changes during growth and sexual dimorphism all require a larger sample size than is presently available. More recently, however, characteristic features of the parasphenoid have been used by various workers in an attempt to work out phylogenetic relationships (GARDINER & MILES, 1990, 1994; CARR, 1991).

The origin of the parasphenoid remains an open question. A number of sources have been suggested, some based on analogy (DUNKLE & BUNGART, 1946) and others on histological evidence (KULCZYCKI, 1957). More recently GOUJET (1984) has presented evidence from transverse sections of *Dicksonosteus* that the parasphenoid has a mixed origin. This view supports STENSIÖ's (1963: 228) suggestion for the origin of the parasphenoid in pholidosteids. However, in both of these forms the parasphenoid is closely associated with the endocranium. This is not the case with, for example, the arthrodires from Gogo where the parasphenoid is easily isolated and both dorsal and ventral surfaces of the bone are available for study. The endocranium is rarely preserved. The origin of the parasphenoid in these latter forms remains uncertain.

With such a small sample size, it is particularly difficult to assess changes that occur during growth or to know whether or not sexual dimorphism, the ageing of mature individuals and/or normal variation are contributing to the differences observed. The parasphenoids of both *Incisoscutum* (9 examples) and *E. calliaspis* (11) vary but, the specimens in which the differences occur, are of very similar size. YOUNG (1979) attributes changes in the shape of the parasphenoid of *Buchanosteus* (7) to growth and variation in the ornament to postmortem damage. In contrast, the parasphenoid of *E. calliaspis* alters very little in shape from the smallest (prepineal length 50.6 mm) to the largest specimen (prepineal length 196.0 mm) (DENNIS, 1984 Ph. D. thesis). LONG (1984) suggests that in *Austrophyllolepis*, juvenile (small) specimens lack the edenticulate region found in the parasphenoid of adults (large). However, this bone is preserved in only two juveniles of each species. As I have not examined this material, and as LONG's (1984, Figs. 5-6) figures are unclear with regard to this feature, I cannot comment further on this matter.

Prior to the utilization of parasphenoid characters for phylogentic analyses, parasphenoids were discussed more in terms of which were primitive 'types' and which were advanced or derived (DENNIS, 1984, Ph. D thesis; GARDINER & MILES, 1990). The primitive parasphenoid is usually flat and without notches or grooves. The ventral surface is covered with tubercles and there is a large median buccohypophysial foramen which may be single or paired. The advanced 'type' is thicker and more structured bearing notches, grooves and foramina. Tubercles are reduced in number and extent or absent. There is usually a well developed median ventral crest. There are two notable exceptions to the above – *Pholidosteus* and the two species of *Austrophyllolepis*. The former is considered to be an advanced arthrodire, but has the so-called primitive parasphenoid and in the latter case the reverse is true. It is perhaps possible that the dorsoventrally flattened phyllolepids are in fact more advanced among placoderms than was first thought.

The parasphenoid appears to be species specific in all placoderms except the phyllolepids which LONG (1984) describes without noting any significant differences. The question therefore remains as to whether any character of this bone can be established that defines a larger phylogenetic group. GOUJET (1984: 237) states that a small, subcircular or triangular parasphenoid pierced by either a single or paired buccohypophysial foramen is a character shared by actinolepids, phlyctaeniids and brachythoracid arthrodires. There are, however, within this group of

arthrodires, parasphenoids of very different shapes and which lack a buccohypophysial foramen e.g. *Pholidosteus, Pachyosteus.*

GARDINER & MILES (1990: 197) suggest that parasphenoids possessing (a), a posterior division of the fossa hypophyseos housing the foramen for the median vein and (b), posterolateral processes are characteristic of *Coccosteus, Harrytoombsia, Goujetosteus* (*Torosteus*), *Kimberleyichthys, Incisoscutum* and *Tubonasus* (see character 22.7 of their 'cladogram,' Fig. 30). These are the only forms in which the parasphenoid is preserved, though other arthrodires are included in the group. However, the parasphenoids of *Coccosteus, Harrytoombsia* and *Incisoscutum* lack posterolateral processes and that of *Tubonasus* (LONG, 1988a, Fig. 3) lacks both features (a) and (b). Conversely, *Eastmanosteus* which is not included in the group has a parasphenoid with both a posterior division of the fossa hypophyseos and posterolateral processes (DENNIS-BRYAN, 1987, Fig. 17A).

GARDINER & MILES (1990) also use the presence of a median crest on the ventral surface of the parasphenoid as part of their character 22.27 (character 58, GARDINER & MILES, 1994). However, this crest is clearly evident on the parasphenoid of a number of other arthrodires e.g. *Bullerichthys, E. calliaspis, Dunkleosteus,* that are excluded from the group. CARR (1991) also uses this character in his data matrix (number 74) but it should be noted that he has scored the crest as being present in both *Rolfosteus* and *Camuropiscis* though the bone is not preserved in these forms.

GARDINER & MILES (1990: 198-199) use a third parasphenoid character in their cladogram to unite among others the arthrodires *Bullerichthys, Bruntonichthys, Erromenosteus, Brachyosteus, Trematosteus* and *Pachyosteus.* The character employed is as follows: 'parasphenoid with strongly developed posterolateral processes which give it great depth and a buccohypophysial depression with both anterior and posterior divisions... paired buccohypophysial depression... well developed posterior shelf. This shelf is found in those forms above *Pholidosteus* in our cladogram.' Only the parasphenoid of *Bullerichthys* conforms with every feature mentioned above. Even *Bruntonichthys,* to which it is thought to be closely related, has a parasphenoid that lacks posterolateral processes. Of the other parasphenoids, that of *Brachyosteus* has not been described, those of *Erromenosteus* and *Trematosteus* are only known in ventral aspect and that of *Pachyosteus* conforms on only one point – it has a posterior shelf. It seems, therefore, that this parasphenoid character is also invalid in the GARDINER and MILES phylogenetic scheme, though it is retained in their 1994 paper (character 67).

GARDINER (1990: 313, character 59) uses part of the above character *i.e.* strongly developed posterolateral processes and a hypophysial depression with anterior and posterior divisions, to define a group of arthrodires that includes *Bullerichthys, Bruntonichthys, Brachyosteus, Simosteus, Trematosteus, Erromenosteus* and *Pachyosteus* and others in which the parasphenoid has not yet been described. The reasons for its removal at this level have already been discussed.

CARR (1991) uses four parasphenoid characters in his data matrix. One, number 74, has already been mentioned, the others are as follows:

— character 71, width to length ratio for the parasphenoid pre– and posthypophysial shelf;
— character 72, parasphenoid posterolateral processes;
— character 73, the presence of a foramen for the median hypophysial vein on the parasphenoid.

The latter character is cited with five others as defining the monophyly of coccosteomorph arthrodires. However, this foramen is present in some parasphenoids of the pachyosteomorph *Eastmanosteus calliaspis* e.g. BM(NH) P51140 and P51229. Other specimens of *E. calliaspis* e.g. BM(NH) P50877 and P50888, have only a groove which passes back on the posterior face of the bone without disappearing from the surface. The variation of this character within a species makes it unlikely to be useful in defining a higher taxonomic level. Such characters should, however, continue to be included in analyses as it is important to present and evaluate *all* the information that is available. Furthermore, the inclusion of new data could alter the significance of such characters.

Despite the number of parasphenoids currently available for study, it seems that we are still unable to satisfactorily explain its structure in terms of placoderm phylogeny. Each, with the exception of *Austrophyllolepis* appears to be species specific e.g. character 14 in the LELIÈVRE *et al.* (1987) cladogram, parasphenoid with long prehypophysial process, refers only to *Melanosteus*. CARR (pers. comm) is currently describing two species of *Dunkleosteus* based on differences in the parasphenoid.

CONCLUSION

On present evidence it seems that the parasphenoid of placoderms is species specific and no feature/character has yet been established that is exclusive to a higher taxonomic level. Another group in which the parasphenoid is being studied in detail is the dipnoans (CLOUTIER, pers. comm). Initial findings indicate that here too there is a high degree of species specificity.

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APPENDIX 1

A Listing of Placoderm parasphenoids described to date.

PLACODERMI

ANTIARCHA

BOTHRIOLEPIDIDAE — *Bothriolepis* sp. (from Gogo Western, Australia)
YOUNG, 1986: 47.

PHYLLOLEPIDA

PHYLLOLEPIDIDAE — *Australlophyllolepis youngi*
LONG, 1983, Figs. 11D, 12C, 16, 18B, 20; p. 282.

Austrophyllolepis ritchiei
LONG, 1983, Figs. 4A, 5, 6, 14B, 17; p. 282.

ACANTHOTHORACI

PALAEACANTHASPIDAE — *Kosoraspis peckai*
GROSS, 1959, Figs. 6A, C, 7; Pl. 6.1; p. 24.
STENSIÖ, 1963, Fig. 12B.

ARTHRODIRA

ACTINOLEPID ARTHRODIRES

ACTINOLEPIDIDAE — *Kujdanowiaspis rectiformis*
STENSIÖ, 1963, Figs. 14, 41.

Kujdanowiaspis buczacziensis (Brotzen)
STENSIÖ, 1942, Figs. 4, 5.

Kujdanowiaspis sp.
STENSIÖ, 1963, Figs. 20A-D, G, 36; p. 57, 93, 95-97, 108, 119-121.

Lehmanosteus hyperboreus
GOUJET, 1984, Fig. 107; p. 227.

PHLYCTAENIID ARTHRODIRES

PHLYCTAENIIDAE — *Arctolepis decipiens* (Woodward) 1891
GOUJET, 1984, Figs. 74, 81; p. 171.

Heintzosteus brevis (Heintz) 1929
GOUJET, 1984, Figs. 91, 98; p. 198.

Dicksonosteus arcticus
GOUJET, 1975, Fig. 4; p. 92.
GOUJET, 1984, Figs. 6, 34-38; p. 107-109.

BRACHYTHORACID ARTHRODIRES
'PRIMITIVE' BRACHYTHORACIDS

BUCHANOSTEIDAE — *Buchanosteus confertituberculatus* (Chapman)
HILLS, 1936, Figs. 4, 5; p. 221-222;
WHITE & TOOMBS, 1972, Figs. 4-11, Pl. 3; p. 385-388;
STENSIÖ, 1963, Figs. 37A, 44A-B; p. 95-100, 108, 121-123, 274;
YOUNG, 1979, Figs. 5, 7A, 12, 17, Pls 4-5; p. 336-340.

HOMOSTEIDAE — *Antineosteus lehmani* Lelièvre 1984
LELIÈVRE, 1988, Figs. 2, 3A-C; p. 289-290.

EUBRACHYTHORACID ARTHRODIRES – COCCOSTEOMORPHS

COCCOSTEIDAE — *Coccosteus cuspidatus* Miller ex Agassiz
MILES & WESTOLL, 1968, Figs. 17A, 18A-B, Pl. 2E; p. 405-408.

CAMUROPISCIDIDAE — *Tubonasus lennardensis* Dennis & Miles 1979a
LONG, 1988, Fig. 3; p. 83-84.
Latocamurus coulthardi
LONG, 1988, Figs. 5, 10B-D, Pl. 2; p. 250-251.

PLOURDOSTEIDAE — *Harrytoombsia elegans*
MILES & DENNIS, 1979, Fig. 13; p. 50-51.
Goujetosteus (Torosteus) tuberculatus
GARDINER & MILES, 1990, Fig. 9; p. 186, 193-194.
Goujetosteus (Torosteus) pulchellus
GARDINER & MILES, 1990, Fig. 24; p. 186, 194.
Kimberleyichthys whybrowi
DENNIS-BRYAN & MILES, 1983, Fig. 4; p. 160-161.
Kimberleyichthys bispicatus
DENNIS-BRYAN & MILES, 1983, Fig. 13; p. 166.
Panxiosteus ocullus
WANG, 1979, Fig. 2; p. 183, 186, 188.
Compagopiscis croucheri
GARDINER & MILES, 1994, Figs. 7, 10D-7; p. 143.
Gogopiscis gracilis
GARDINER & MILES, 1994, Fig. 17; p. 462-465.

PHOLIDOSTEIDAE — *Pholidosteus bidorsatus* (v. Koenen)
STENSIÖ, 1963, Figs. 49B-C, 51C, 75; p. 172-173, 211, 228, 302.
Tapinosteus heintzi Stensiö 1959
STENSIÖ, 1963, Figs. 48, 50A, D, E, 53A, 55C, D, 56B-D, 58, 63, 71; p. 169-173, 211, 228, 302.
Malerosteus gorizdroae
KULCZYCKI, 1956, Pls 1H, 2, Figs. 1-2; p. 104-106.
KULCZYCKI, 1957: 297.

EUBRACHTYTHORACID ARTHRODIRES – PACHYOSTEOMORPHS

DINICHTHYIDAE — *Dunkleosteus terrelli* (Newberry)
DUNKLE & BUNGART, 1946, fig. 3A, B; p. 6.
STENSIÖ, 1963, Figs. 114A-C, 115A; p. 271-272, 354-356.

	Dunkleosteus? sp.	LEHMAN, 1956, Pl.10, fig. 3; p. 38.
	Eastmanosteus calliaspis	DENNIS-BRYAN, 1987, Figs. 9A, 17; p. 27-28.
	Heintzichthys gouldii (Newberry)	DUNKLE & BUNGART, 1946, Fig. 3C, D; p. 6. STENSIÖ, 1963, Figs. 114D-F; p. 271– 272, 356. CARR, 1991, Fig. 8A-C; p. 361.
	Kiangyousteus yohii	LIU, 1955, Fig. 1, Pl. 2; p. 3 described as a pineal. DENISON, 1978, Fig. 71; p. 91.
SELENOSTEIDAE	*Melanosteus occitanus* Lelièvre & Goujet, 1987	LELIÈVRE, FEIST, GOUJET & BLIECK, 1987, Pl. 2 C-E; p. 13.
	Pachyosteus bulla Jaekel, 1927	KULCZYCKI, 1957, Fig. 13; p. 326. STENSIÖ, 1963, Fig. 115H-J; p. 271, 274, 302, 356-357.
LEIOSTEIDAE	*Erromenosteus lucifer* Jaekel, 1927	STENSIÖ, 1945: 67. STENSIÖ, 1963, Fig. 115E-G; p. 272, 354.
TREMATOSTEIDAE	*Trematosteus fontanellus* Gross, 1932	STENSIÖ, 1945: 67. STENSIÖ, 1963, Figs. 87A, D, 91D, 92A, B; p. 271-272, 352-353.
	Brachyosteus dietrichi Gross, 1932	STENSIÖ, 1945: 67. STENSIÖ, 1963: 354-356.
Family indet.	*Incisoscutum ritchei*	DENNIS & MILES, 1981, Figs. 14-15; p. 235.
	Tafilalichthys lavocati Lehman, 1956	LELIÈVRE, 1991, Fig. 4; p. 124.
	Simosteus tuberculatus	DENNIS & MILES, 1982, Fig. 5C; p. 163.
Kendrickichthyid arthrodires	*Bruntonichthys multidens*	DENNIS & MILES, 1980, Figs. 1, 2, 3C-D; p. 51.
	Bullerichthys fascidens	DENNIS & MILES, 1980, Fig. 9; p. 58-59.

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Section C, n° 1-4 : 143-161.

The brachial articulation and pectoral fin in Antiarchs (Placodermi)

by Philippe JANVIER

Abstract. — The structure of the articulation for the pectoral fin in the Antiarcha is reviewed, with particular reference to the Early Devonian taxa from China, Vietnam and Australia: the Yunnanolepiformes, Procondylolepiformes and Sinolepidae. The Sinolepidae display an amazing diversity of structure of the brachial articulation area of the anterior ventrolateral plate, ranging from a very simple structure, like that of the Yunnanolepiformes, to more complex ones resembling quite closely that of the Euantiarchi. This suggests that the Sinolepidae may not be monophyletic, and that their presumed autapomorphy (the large ventral fenestration of the thoracic armour) could be either plesiomorphous for the Antiarcha or for the ensemble Sinolepidae + Euantiarchi, or also homoplastic in *Vanchienolepis*, *Xichonolepis* and *Sinolepis*. The pectoral fin exoskeleton is described in a *Vanchienolepis*-like specimen from Yunnan, and a possible pectoral fin, partly covered with scales or minute platelets is described in a specimen of *Yunnanolepis* from Vietnam.

Keywords. — Antiarcha, Yunnanolepiformes, Procondylolepiformes, Sinolepidae, brachial articulation.

L'articulation brachiale et la nageoire pectorale chez les Antiarches (Placodermi)

Résumé. — La structure de l'articulation brachiale des Antiarches est décrite, en particulier chez des formes du Dévonien inférieur de Chine, du Viêt-Nam et d'Australie : les Yunnanolépiformes, Procondylolépiformes et sinolépidés. Les sinolépidés présentent une étonnante diversité dans la structure de la zone d'articulation brachiale portée par la plaque ventrolatérale antérieure. Celle-ci va d'une structure très simple, assez comparable à celle des Yunnanolépiformes, jusqu'à une structure beaucoup plus complexe et très voisine de celle des Euantiarches, suggérant ainsi que les sinolépidés, définis par la présence d'une large fenestration ventrale de la cuirasse thoracique, ne sont peut-être pas monophylétiques. Dans ce cas, leur autapomorphie présumée pourrait être soit un caractère plésiomorphe pour les antiarches ou pour l'ensemble sinolépidés + euantiarches, soit une homoplasie chez *Vanchienolepis*, *Xichonolepis* et *Sinolepis*.

Mots-clés. — Antiarcha, Yunnanolépiformes, Procondylolépiformes, Sinolepidae, articulation brachiale.

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INTRODUCTION

The Antiarcha is a monophyletic group of placoderms characterized by e.g. a derived structure of the pectoral fins, which consists of generally jointed appendages enclosed in a rigid sheath of dermal platelets, and which articulates directly with the anterior ventrolateral plate (thereafter called AVL) of the thoracic armour. Since Hugh MILLER (1841), and until the 1960ies, the antiarchs had been recorded from many Middle and Late Devonian localities of Europe,

North America, Asia, Australia and Antarctica, but were shown to be quite homogeneous in structure. Two major groups, the Bothriolepidoidei and Asterolepidoidei, were distinguished, both possessing jointed pectoral appendages, with one exception: the Late Devonian asterolepidoid genus *Remigolepis* whose appendages are unjointed. Also, in both groups, the exoskeletal component of the pectoral fin articulates on the AVL plate by the means of a ball-and-socket device, the ball being an helmet-shaped brachial process (brp, Fig. 1D) of the AVL plate. The vascularization and innervation of the fin was effected through a large axillary foramen (axf, Fig. 1D)

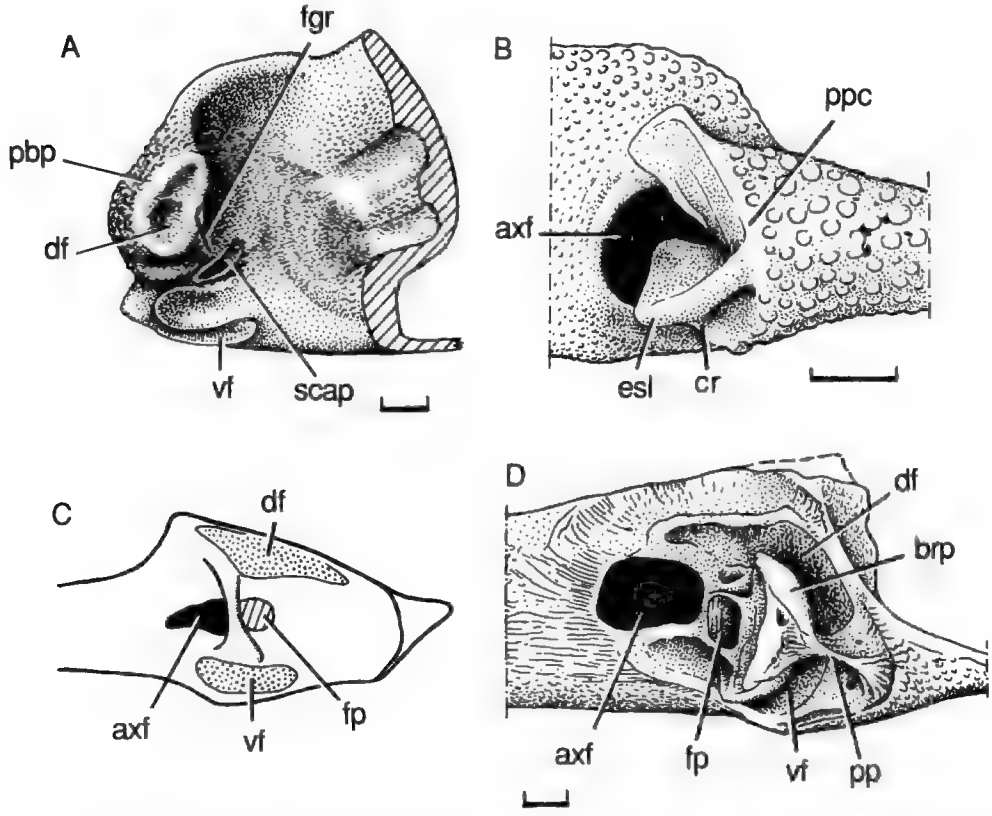


FIG. 1. — The brachial articulation area of the anterior ventrolateral plate (AVL) in the Antiarcha. A, *Chuchinolepis dongmoensis* Tong Dzuy & Janvier, Early Devonian of Vietnam, posterior view (from TONG DZUY & JANVIER, 1990, modified after further preparation of UHDG-VND27d). B, *Vanchienolepis langsonensis* Tong Dzuy & Janvier, Early Devonian of Vietnam, lateral view (based mainly on specimen UHDG-VND47 in Figure 5C). C, *Grenfellaspis*, Late Devonian of Australia (from YOUNG & ZHANG, 1992). D, *Bothriolepis macphersoni* Young, Devonian of Antarctica (from YOUNG 1988). Scale bar: 1 mm for A, B, and 5 mm for D.

Région de l'articulation brachiale de la plaque ventrolatérale antérieure (AVL) des Antiarcha. A, Chuchinolepis dongmoensis *Tong Dzuy & Janvier, Dévonien inférieur du Viêt-Nam, vue postérieure (d'après TONG DZUY & JANVIER, 1990, modifié par une préparation supplémentaire de UHDG-VND27d). B,* Vanchienolepis langsonensis *Tong Dzuy & Janvier, Dévonien inférieur du Viêt-Nam, vue latérale (principalement d'après le spécimen UHDG-VND47 de la figure 5C). C,* Grenfellaspis, *Dévonien supérieur d'Australie (d'après YOUNG & ZHANG, 1992). D,* Bothriolepis macphersoni *Young, Dévonien de l'Antarctique (d'après YOUNG, 1988). Échelle : 1 mm pour A, B, et 5 mm pour D.*

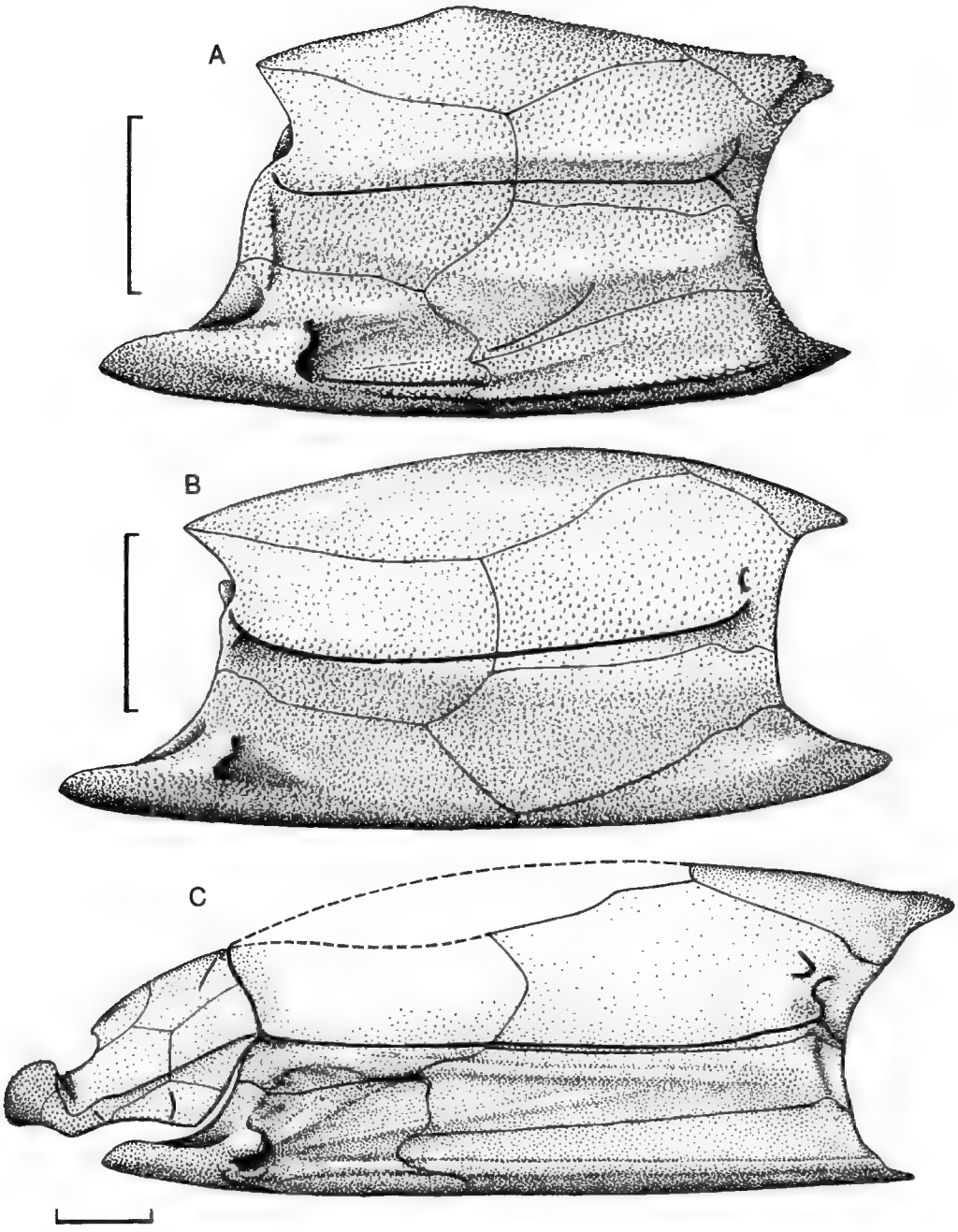
piercing the AVL plate behind the brachial process. Thanks to STENSIÖ's (1948) thorough description of the bothriolepid *Bothriolepis canadensis* from the Late Devonian of Miguasha, Québec, the structure of the rather complex ball-and-socket brachial articulation of advanced antiarchs is now well known. It has been completed by detailed studies on the asterolepid *Asterolepis ornata* from Latvia (GROSS, 1931; LYARSKAYA, 1981) and bothriolepids from Australia (YOUNG & ZHANG, 1992). However, virtually nothing was known of the endoskeleton of antiarchs, until the discovery of perichondrally ossified mandibular arch elements in a *Bothriolepis* specimen from the Late Devonian of Australia (YOUNG, 1984a).

As early as 1958, a peculiar antiarch, *Sinolepis macrocephala*, was described by LIU & PAN (1958) from the Devonian of China, but, since it possessed typical jointed appendages, similar to those of the Bothriolepidoidei, the unusual structure of its skull-roof (in particular the very elongated nuchal plate, and the preorbital depression) did not raise much attention. Nevertheless, it was placed in a family of its own, the Sinolepidae.

In the early 1960's, some even more peculiar antiarchs were discovered in the Early Devonian of Yunnan, China (LIU, 1963). They differed from all previously known antiarchs by the lack of a complex brachial articulation, and by a number of features in their skull-roof that could be regarded as primitive (long nuchal and short premedian plates). Dr. CHANG Mee mann (Beijing) was studying this remarkable material in Stockholm when the "Great Cultural Revolution" broke out. She had to return to China with her still unpublished material, part of which appeared in print only in 1978 in two papers by CHANG KUO JUI (1978) and ZHANG GUORUI (= CHANG KUO-JUI) (1978) respectively. A more detailed description of the same specimens by CHANG Mee mann appeared two years later (M.M. ZHANG, 1980). These papers revealed the morphology of what is now regarded as the most primitive antiarchs, the Yunnanolepiformes (*Yunnanolepis, Phymolepis*), which are possibly a paraphyletic group (TONG DZUY & JANVIER, 1990). The Yunnanolepiformes differed from all previously known antiarchs by the lack of a brachial process and axillary foramen, their area for the articulation of the pectoral fin, or pectoral fenestra, being a mere recess in the AVL plate (Fig. 2A, B)

There was no known intermediate between the typical ball-and-socket brachial articulation of the Euantiarchi (Bothriolepidoidea and Asterolepidoidea) and the very simple structure in the Yunnanolepiformes until 1984, when ZHANG GUORUI described a new genus, *Procondylolepis*, found in association with the Yunnanolepiformes in the Early Devonian of Yunnan. *Procondylolepis* and the closely related genus *Chuchinolepis*, display a sort of process prolonging the prepectoral corner (pbp, Fig. 1A), yet not shaped like that of the Euantiarchi and lacking a large axillary foramen for the passage of the brachial nerves and blood vessels. These seemed to have passed through minute foramina piercing the brachial articulation area (f, Figs. 4, 8). By this time, cladistic analyses of a number of characters of the skull-roof and thoracic armour clearly suggested that the Sinolepidae were the sister-group of either the Euantiarchi (JANVIER & PAN, 1982) or the Bothriolepidoidei (YOUNG, 1984b, 1988). It could thus be predicted that, when discovered, the brachial process of the Sinolepidae might appear to be either intermediate between that of *Procondylolepis* and that of the Euantiarchi, or simply identical to that of either the former or the latter.

The recent dicovery of a rich Early Devonian antiarch fauna in northern Vietnam (TONG DZUY & JANVIER, 1990) has provided new data which do not really meet these expectations.


A
B
C

This fauna comprises typical yunnanolepiforms (*Yunnanolepis*, Fig. 2A, B), a procondylolepiform (*Chuchinolepis*, Fig. 2C), and a small form referred to the Sinolepidae, *Vanchienolepis* (Figs. 1B, 5B-D), in which the dermal brachial articulation area could be observed. The latter shows no resemblance to either that of the Procondylolepiformes or that of the Euantiarchi, apart from the presence of an axillary foramen, which rather recalls the Euantiarchi (axf, Fig. 1B). At the same time, the brachial articulation of a new sinolepid, *Grenfellaspis*, from the Late Devonian of Australia has been described, showing another type of brachial process (Fig. 1C; RITCHIE, *et al.*, 1992; YOUNG & ZHANG, 1992). Finally, yet another type of brachial articulation area is described in a sinolepid-like anterior ventrolateral plate from Wuding, Yunnan, China (Fig. 7)

Four questions then arose:

1– What are the homologies between the various structures observed in the brachial articulation area of antiarchs?

2 – How did the fin plates articulate with the anterior ventrolateral plate in the various antiarchan groups?

3 – Are the Sinolepidae monophyletic?

4 – At which level of the cladogram of the Antiarcha does the appendage-like pectoral fin structure appear?

YOUNG & ZHANG (1992) recently published a paper which answers the first two questions, and is largely convergent with the results I presented during the Miguasha symposium.

The data presented in this paper are taken from three sources of material: Early Devonian (most probably Late Lochkovian or Early Pragian) antiarchs from Vietnam and China, and an Eifelian antiarch from Iran. The material from Vietnam (*Yunnanolepis*, *Chuchinolepis*, *Vanchienolepis*) is from the localities of Dong Mo and Trang Xa (Lang Son and Bac Thai districts respectively) and has been collected in a collaboration between the University of Hanoi and the Laboratoire de Paléontologie, MNHN, Paris. The material from China has been collected by H. LELIÈVRE and D. GOUJET (Paris) during the excursion of the meeting on "Early Vertebrates and Related Problems of Evolutionary Biology" (Beijing, 1987). The material from Vietnam belongs to the collection of the Department of Geology of Hanoi University, Vietnam (UHDG). The material from China is registered in the Collections of the Museum National d'Histoire Naturelle, Paris (MNHN). The material from Iran belongs to the Museum of the Geological Survey of Iran, Tehran (MGSI).

The material from Vietnam has been prepared with an air-abrasive as well as mechanically, with a needle. The material from China has been prepared chemically, with 10% formic acid.

FIG. 2. — Dermal thoracic armour of two Yunnanolepiformes (A, B) and a Procondylolepiforme (C) from the Early Devonian of Dong Mo, Lang Son, Vietnam, in lateral view, showing the brachial articular area. A, *Yunnanolepis bacboensis* Tong Dzuy & Janvier. B, *Y. deprati* Tong Dzuy & Janvier. C, *Chuchinolepis dongmoensis* Tong Dzuy & Janvier (skull-roof added), (from TONG DZUY & JANVIER, 1990). Scale bar: 10 mm.

Cuirasse thoracique de deux Yunnanolépiformes (A, B) et d'un Procondylolépiforme (C) du Dévonien inférieur de Dong Mo, Lang Son, Viêt-Nam, en vue latérale pour montrer la région de l'articulation brachiale. A, Yunnanolepis bacboensis *Tong Dzuy & Janvier*. B, Y. deprati *Tong Dzuy & Janvier*. C, Chuchinolepis dongmoensis *Tong Dzuy & Janvier (toit crânien ajouté) (d'après TONG DZUY & JANVIER, 1990). Échelle : 10 mm.*

The material from Iran is preserved as impressions, and casts of the natural moulds have been made with silicone rubber.

ABBREVIATIONS

adr	anterodorsal ridge, *ride antérodorsale*;
apr	ornamented "apron" on anterior surface of internal transverse crest (postbranchial lamina), *"apron" ornementé sur la surface antérieure de la crête transverse (lame postbranchiale)*;
axf	axillary foramen, *foramen axillaire*;
bra	brachial articulation area, *région de l'articulation brachiale*;
brc	brachial canal for blood vessels and nerves, *canal brachial pour vaisseaux sanguins et nerfs*;
brp	brachial process, *processus brachial*;
Cd, Cv	proximal dorsal and ventral central plates of appendage, *plaques centrales proximale dorsale et proximale ventrale*;
cit	transverse internal crest, *crête transverse interne*;
cr	presumed pedal crest, *crête ventrale présumée*;
cr	ventral crest (or pedal crest), *crête ventrale*;
df	dorsal articular fossa, *fosse articulaire dorsale*;
esl	ear-shaped lamina, *lame en forme d'oreille*;
f	foramina for brachial nerves and blood vessels, *foramina pour les nerfs brachiaux et les vaisseaux sanguins*;
fgr	groove on medial surface of the parabrachial process, possibly corresponding to the lateral wall of the funnel pit, *sillon sur la surface médiale du processus parabrachial*;
fp	funnel pit, *ouverture en entonnoir*;
fpl	tile-shaped fin plates, *plaques des nageoires en forme de tuile*;
fsc	fin scales, *écailles des nageoires*;
Ml, Mm	lateral and medial marginal plates of appendage, *plaques marginales latérale et médiale de l'appendice*;
n	notch for a process of the posterior ventrolateral plate, *encoche pour un processus de la plaque ventrolatérale postérieure*;
pbp	parabrachial process, *processus parabrachial*;
PDL	posterior dorsolateral plate, *plaque postérodorsale*;
PL	posterolatral plate, *plaque postérolatérale*;
pp	pedal part of brachial process, *partie pédieuse du processus brachial*;
ppc	prepectoral corner, *angle prépectoral*;
PVL	posterior ventrolatral plate, *plaque ventrolatérale postérieure*;
pvr	posteroventral ridge, *ride ventrale postérieure*;
r	recess lying behind the transverse internal crest, *recessus en arrière de la crête transverse interne*;
scap	funnel-shaped perichondral bone of the scapulocoracoid, *os perichondral du scapulocoracoïde*;

scap	perichondral bone of scapulocoracoid, *os périchondral en forme de trémis du scapulocoracoïde*;
vf	ventral articular fossa, *fosse articulaire ventrale*;
vfe	ventral fenestration in the thoracic armour, *fenestration ventrale de la cuirasse thoracique.*

THE BRACHIAL ARTICULATION AREA OF THE AVL PLATE

The area of the AVL plate on which the pectoral fin or appendage articulates is now fairly well known in a wide range of antiarchan taxa. It comprises the pectoral fenestra proper (scap, Figs. 1A, 4), lined with the perichondral bone of the scapulocoracoid (this area being, however, much reduced in most antiarchs), and the dermal articular area on which the fin plates articulate with the AVL plate. It is briefly described here in order of what is generally believed to be an order of increasing complexity.

YUNNANOLEPIFORMES

The brachial articulation is known in various species of *Yunnanolepis* (M.M. ZHANG, 1980; TONG DZUY & JANVIER, 1990) and displays virtually the same structure. It is a small recess corresponding essentially to the pectoral fenestra in the AVL plate (bra, Fig. 3.8), with no conspicuous crest or process, other than a pointed prolongation of the prepectoral corner of the plate (Fig. 2A, B). The main question about this type of brachial articulation area is how nerves and blood vessels passed from the brachial plexi toward the pectoral fin. Grinding serial sections of the AVL plate of *Yunnanolepis deprati* from Vietnam show a minute canal which may have played this role (brc, Fig. 3.3). This canal is issued from the internal recess (r, Fig. 3.1) which is limited anteriorly by the postbranchial lamina (or anterior transverse crest, cit, Fig. 3.3) of the AVL plate, then it bends posterolaterally toward the pectoral fenestra. One particular detail is worth noticing: this canal is lined by a thickened sheath of bone, which looks like perichondral bone. When reaching the brachial recess, this canal widens and its lining seems to continue for a short distance beyond the wall of the recess (Fig. 3.6, 7) a condition which suggests that it was still surrounded by cartilage. One may thus suggest that the brachial recess was, at least in part, filled with a cartilaginous plug (possibly a remnant of the scapulocoracoid) on which the endoskeleton of the pectoral fin could articulate. At this level, the proximal dermal plates of the fin may not have played a role in the brachial articulation (YOUNG & ZHANG, 1992). At least, in *Phymolepis* (G.R. ZHANG, 1978; M.M. ZHANG, 1980), there seems to be no trace of a dermal articulation between the fin plates and the AVL plate. Whether the pectoral fins of the Yunnanolepiformes were already jointed appendages is not known, but a specimen from the Lower Devonian of Vietnam (see below, Fig. 8) may suggest that its distal end was still scale-covered and mobile.

The brachial recess in some Yunnanolepiformes (in particular *Y. deprati*, Fig. 2B) is so small (its breadth is 2 mm for a 2 cm long AVL plate) that one may wonder if the fin was not on the verge to disappearance in at least some members of the group (a parallel with trematapsids among osteostracans).

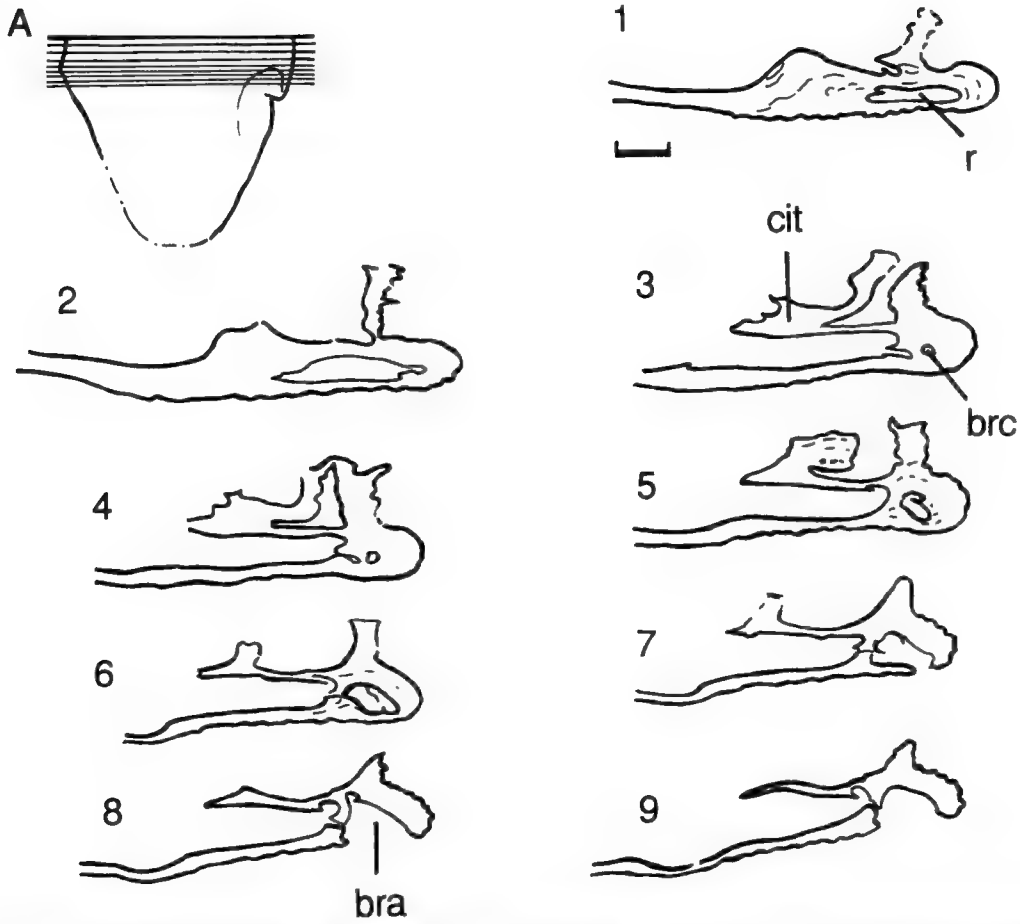


FIG. 3. — *Yunnanolepis deprati* Tong Dzuy & Janvier. Early Devonian of Vietnam, transverse serial grinding sections through the anterior ventrolateral plate (UHDG-VND27o). A, outline of the plate, showing the levels of the respective sections (1 to 9, from front to rear). Scale bar: 1 mm.

Yunnanolepis deprati *Tong Dzuy & Janvier, Dévonien inférieur du Viêt-Nam, sections sériées transverses à travers la plaque ventrolatérale antérieure (UHDG-VND27o). A, contour de la plaque montrant les différents niveaux des sections (1 à 9 de l'arrière vers l'avant). Échelle : 1 mm.*

PROCONDYLOLEPIFORMES

The brachial articulation of the Procondylolepiformes has been described first in *Procondylolepis* (G.R. ZHANG, 1984; YOUNG & ZHANG, 1992) and later in *Chuchinolepis* (TONG DZUY & JANVIER, 1990, Figs. 1A, 2C, 4), these two genera being closely related or even possibly synonymous. There, the articulation area of the AVL plate is much larger, the prepectoral corner being produced into a massive process, the parabrachial process (pbp, Figs. 1A, 4), hollowed distally by a piriform depression (df, Figs. 1A, 4.4). The wall of this area bears, in addition, a

number of ridges and grooves which YOUNG & ZHANG (1992) have homologized with the structures observed in the Euantiarchi. In this taxon, like in the Yunnanolepiformes, the pectoral fenestra proper is filled with the perichondral bone of the scapulocaracoid (scap, Figs. 1A, 4.7) and pierced by foramina for the vessels and nerves to the pectoral fin (f, Fig. 4.8). All the details recorded by ZHANG (1984) and YOUNG & ZHANG (1992) in *Procondylolepis* could be confirmed by the grinding sections through the AVL plate of *Chuchinolepis dongmoensis* from Vietnam (Fig. 4).

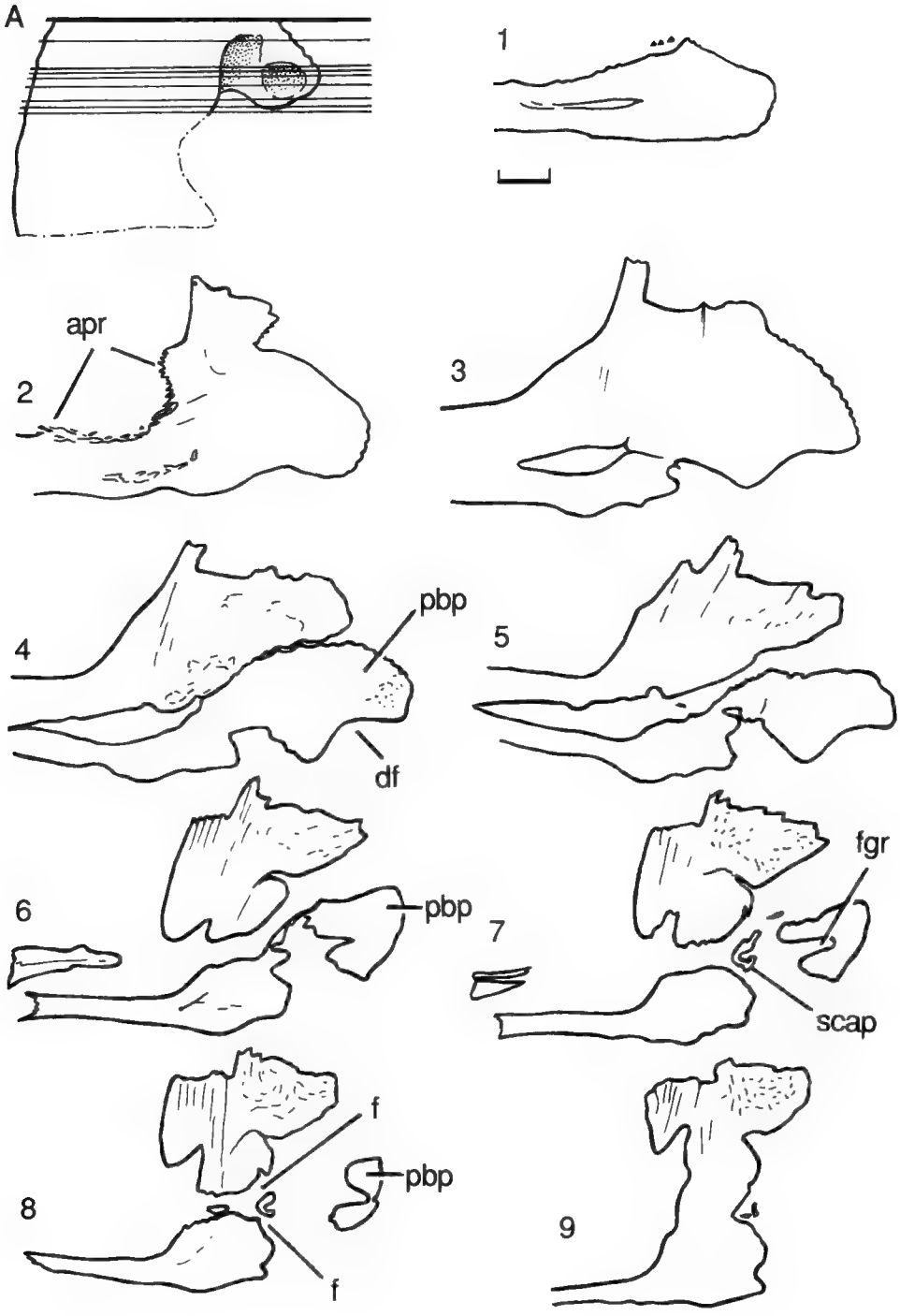
G. R. ZHANG (1984) has also described the proximal portion of the pectoral appendage-like fin of *Procondylolepis*, though not articulated with the AVL plate and he proposed one possible way in which this fin could articulate to the brachial recess. In both the Chinese and the Vietnamese procondylolepiform material, one of the proximal plates of the pectoral fin bears a spoon-shaped knob which is likely to have been housed in the part of the articulation area that YOUNG and ZHANG (1982) regard as homologous to the ventral articular fossa of the Euantiarchi (vf, Fig. 1A, C), the dorsal one (Fig. 1D) being the piriform depression on the tip of the parabrachial process (df, Figs. 1A, 4.4)

ZHANG (1984) suggested that the process in the Procondylolepiformes is homologous to the brachial process of the Euantiarchi. In contrast, TONG DZUY & JANVIER (1990), termed it as the "parabrachial process" (pbp, Fig. 1A), and regarded it as too dorsal in position to be the brachial process proper. YOUNG & ZHANG (1992) now propose a hypothesis of homology which seems quite satisfactory, considering that the groove on the medial side of the parabrachial process (fgr, Figs. 1A, 4.7) corresponds to part of the wall of the "funnel pit" in the Euantiarchi (fp, Fig. 1D). In fact, in both case, the wall of the groove and the pit are marked by particular growth lines found nowhere else in this area. However, if one considers that the parabrachial process is the homologue of the brachial process of the Euantiarchi, its distal depression could correspond to the area of insertion for the protractor muscle of the pectoral appendages.

The Procondylolepiformes are now known from almost complete specimens of *Chuchinolepis* (TONG DZUY & JANVIER, 1990; Fig. 2C), which suggest that they are more closely related to Euantiarchi than to the Yunnanolepiformes. However, this group has many autapomorphies, such as the very short AVL plates, very long AMD plate, and very fine-grained ornamentation.

SINOLEPIDAE

Sinolepis macrocephala (LIU & PAN, 1958), from the Late Devonian of China, has long been the only known species of this group, which allies elongated nuchal plates and a large preorbital depression in the skull-roof, with bothriolepidoid-like thoracic armour and paired appendages. For this reason, it was regarded by JANVIER & PAN (1982) as the sister-group of the Euantiarchi. LONG (1983) erected the taxon Sinolepidoidei for *Sinolepis* and possibly *Xichonolepis*, defined by very narrow ventral lamina of the AVL and PVL plates. Later, YOUNG (1984b) characterized the Sinolepidae by a large ventral fenestration in the thoracic armour, and included in this family the genera *Sinolepis*, *Xichonolepis*, *Dayaoshania* and *Liujiangolepis* from the Late and Early Devonian of China, and *Grenfellaspis*, from the Late Devonian of Australia (RITCHIE *et al.*, 1992; see this article for details on the in-group phylogeny). TONG DZUY & JANVIER (1990) added to this family *Vanchienolepis*, from the Early Devonian of Vietnam. Like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all other sinolepids, *Vanchienolepis* has a large ventral fenestra in the thoracic armour and, thus, no median ventral plate. Thanks to the excellent preservation of the material from Dong Mo, Vietnam, the brachial articulation area of this minute form could be observed (Figs. 1B, 5B-D). It displays a relatively large axillary foramen (axf, Fig. 1B), like in the Euantiarchi, but the articulation area proper is quite different from both the Procondylolepiformes and the Euantiarchi. There is neither a parabrachial nor a true brachial process and the prepectoral corner lines a deep, almost conical depression, possibly for the abductor muscles of the fin. In the ventral part of the latter arises an ear-shaped dermal lamina (esl, Figs. 1B, 5B), the ventral surface of which is connected to the margin of the articulation area by a short ridge or crest which separates two shallow depressions (cr, Figs. 1B, 5B). The bottom of the cone-shaped depression in the centre of the area seems to be pierced by a minute canal. In addition, D. GOUJET (Paris) has kindly permitted me to study a well preserved small antiarch from the Early Devonian of Qujing, China, which displays very much the same characters as *Vanchienolepis* and is preserved with the proximal part of the right pectoral fin in its natural position (Fig. 6, see below).

A comparison between the brachial articulation area of *Vanchienolepis* and that of *Hyrcanaspis*, a supposedly primitive euantiarch from the Eifelian of Khush-Yeilagh, Iran, may suggest that the ventrally placed pedal part of the brachial process in *Hyrcanaspis* (pp, Fig. 5A) corresponds to the small ridge which, in *Vanchienolepis* and the Chinese form just mentioned, connects the ear-shaped lamina to the margin of the articulation area (cr, Figs. 1B, 5B, 6A-B). This hypothesis of homology implies that the ear-shaped lamina could be the brachial process in a primitive state. But in this case, we meet again with the problem of the comparison to the Procondylolepiformes. YOUNG & ZHANG (1992) model of homology implies that a very large ventral articular fossa is primitive for the Euantiarchi, whereas the supposedly primitive Euantiarchi, such as *Hyrcanaspis* have a ventrally placed pedal ridge, which separates a small to moderately large ventral fossa (vf, Fig. 5A), from a very large dorsal fossa (df, Fig. 5A). TONG DZUY & JANVIER (1990) suggested that the ear-shaped lamina of *Vanchienolepis* could be represented in the Procondylolepiformes by the "ventral crescentiform ridge" which lines dorsally the ventral articular fossa (vf, Fig. 1A) and occupies very much the same position. However, nothing more than topological arguments supports this statement. Another possibility (G. YOUNG, pers. comm.) could be that the large process which prolongs posterodorsally the prepectoral corner in *Vanchienolepis* is the homologue of the parabrachial process of the Procondylolepiformes and of the dorsal articulation of *Grenfellaspis*.

A further variation of the sinolepid brachial articulation is shown by a peculiar AVL plate of an undetermined sinolepid from Qujing, China (Fig. 7). It has a large median ventral fenestration (vfe, Fig. 7), the presumed sinolepid autapomorphy, but otherwise differs markedly from the AVL in both *Vanchienolepis* (Figs. 1B, 5C) and *Grenfellaspis* (Fig. 1C). The lateral lamina of the plate is embayed by a deep longitudinal notch, reaching as far anteriorly as the brachial

FIG. 4. — *Chuchinolepis dongmoensis* Tong Dzuy & Janvier, Early Devonian of Vietnam, transverse serial grinding sections through the anterior ventrolateral plate (UHDG-VND27m). A, outline of the plate, showing the level of the respective sections (1 to 9, from front to rear). Scale bar: 1 mm.

Chuchinolepis dongmoensis *Tong Dzuy & Janvier, Dévonien inférieur du Viêt-Nam, sections sériées transverses à travers la plaque ventrolatérale antérieure (UHDG-VND27m). A, contour de la plaque montrant les différents niveaux des sections (1 à 9 de l'avant vers l'arrière). Échelle : 1 mm.*

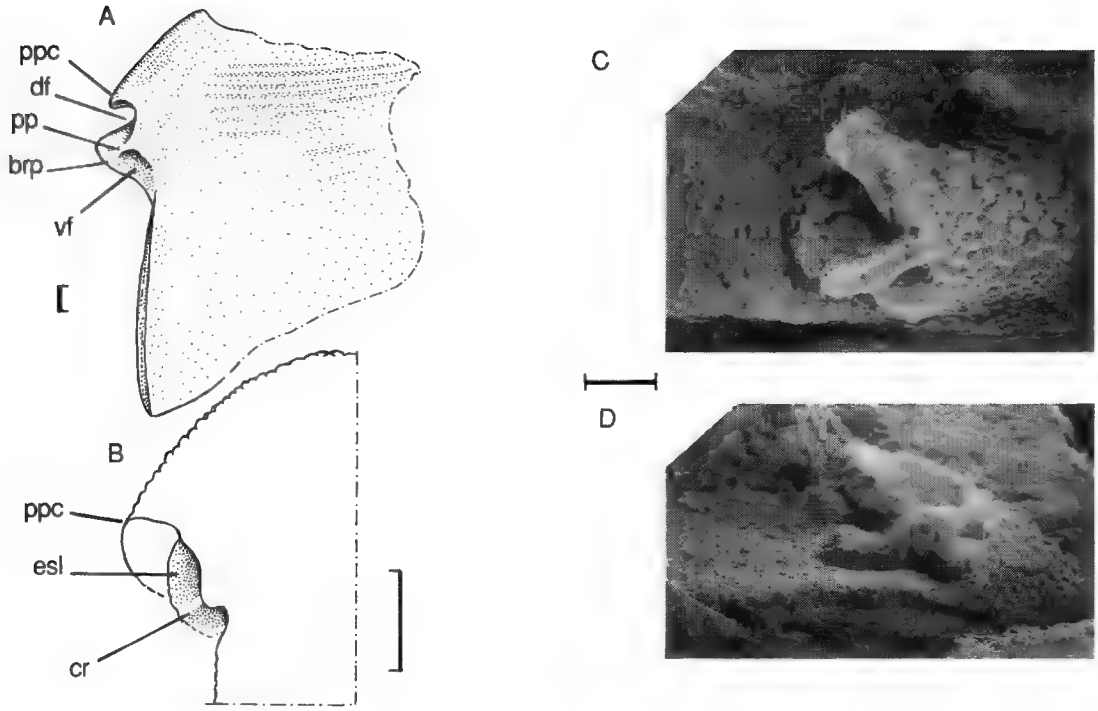
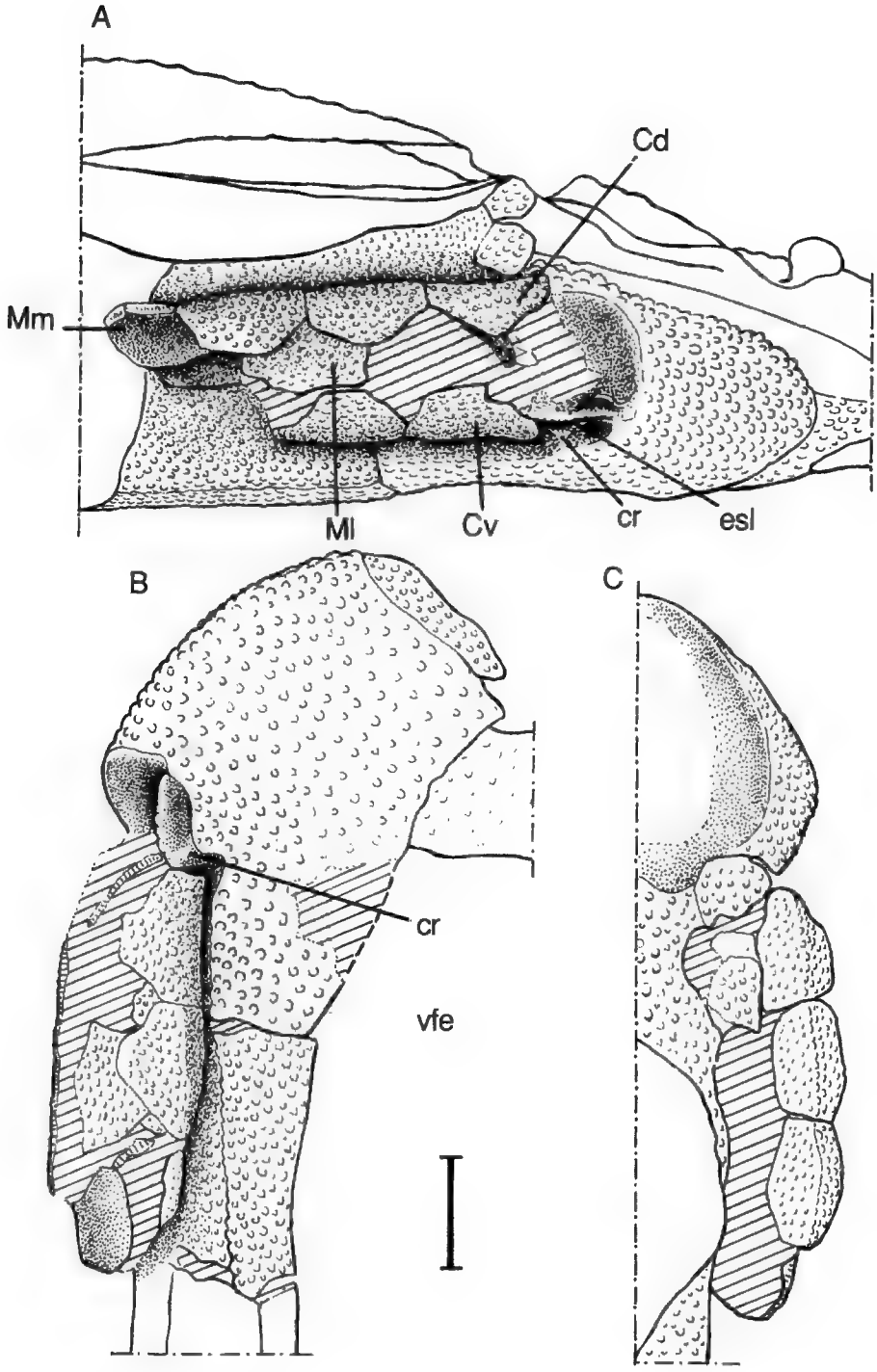


FIG. 5. — A, *Hyrcanaspis bliecki* Janvier & Pan, Middle Devonian of Iran, right anterior ventrolateral plate in ventral aspect, showing the brachial process (MGSI 151, from Janvier & Pan 1982). B, *Vanchienolepis* sp., Qujing, Yunnan, China, right AVL plate in ventral aspect, showing the "ear-shaped lamina" (based on MNHN-CHD01). C, D, *Vanchienoplepis langsonensis* Tong Dzuy & Janvier, Early Devonian of Dong Mo, Vietnam, S.E.M. photograph of the brachial articulation area of the right AVL plate in lateral (C) and ventral (D) aspects; the specimen has been prepared with the transfer method, and the axillary fenestra is filled with silicone (UHDG-VND46a). Scale bar: 1 mm.

A, Hyrcanaspis bliecki *Janvier & Pan. Dévonien moyen d'Iran, plaque ventrolatérale antérieure en vue ventrale, montrant le processus brachial (MGSI 151, d'après Janvier & Pan 1982). B.* Vanchienolepis *sp., Qujing, Yunnan, Chine, plaque AVL droite en vue ventrale montrant "la lame en forme d'oreille" (d'après MNHN-CHD 01). C, D.* Vanchienoplepis langsonensis *Tong Dzuy & Janvier. Dévonien inférieur de Dong Mo, Viêt-Nam, photographie de la région de l'articulation brachiale d'une plaque AVL droite prise au S.E.M., en vue latérale. (C) en vue ventrale (D); les spécimens ont été préparés par la méthode de transfert, et la fenêtre axillaire est remplie de silicone (UHDG-VND46a). Échelle : 1 mm.*

FIG. 6. — *Vanchienolepis* sp., Early Devonian of Qujing, Yunnan, China (MNHN-CHD01), anterior ventrolateral plate and pectoral appendage of the right side of imperfect dermal armour in lateral (A), ventral (B) and dorsal (C) aspects. Areas filled with matrix obliquely hatched, other plates of the armour in white. Camera lucida drawing. Scale bar: 1 mm.

Vanchienolepis *sp., Dévonien inférieur de Qujing, Yunnan, Chine (MNHN-CHD 01), plaque ventrolatérale antérieure et appendice pectoral droits d'une cuirasse thoracique mal conservée, (A) en vue latérale, (B) en vue ventrale, (C) en vue dorsale. Les régions non dégagées sont hachurées. Dessin à la chambre claire. Échelle : 1 mm.*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articulation area, and the margins of which indicate (by the presence of an overlap area) that it was partly filled by a corresponding process of the PVL plate (n, Fig. 7). However, the foremost part of this notch has smooth margins, and corresponds in position to the axillary foramen. The prepectoral corner is very much like in *Vanchienolepis*, that is, broadly rounded in shape (ppc, Fig. 7A), and there is also a clear funnel-shaped depression, lined with perichondral bone and

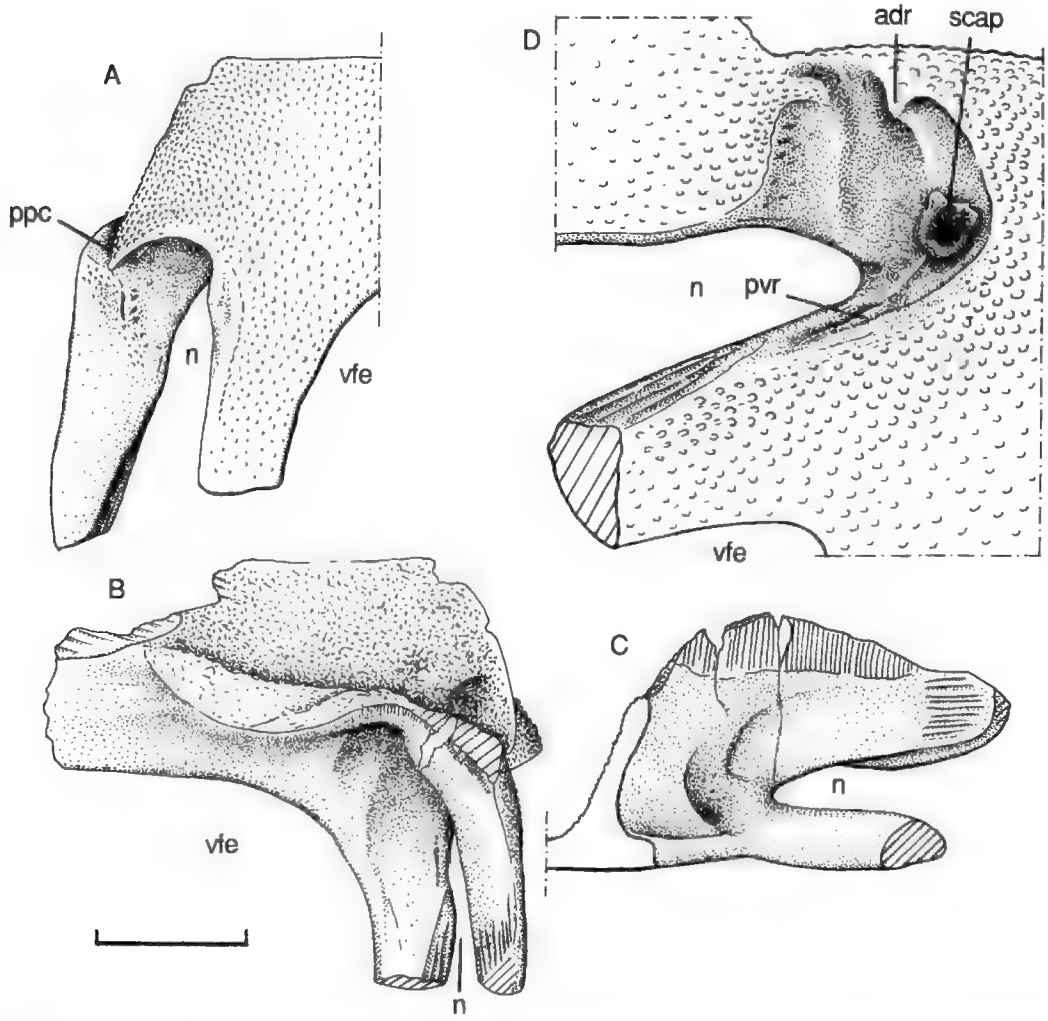


FIG. 7. — ?*Xichonelepis* sp., Early Devonian of Qujing, Yunnan, China (MNHN CHD 02), right anterior ventrolateral plate in ventral (A), dorsal (B) and medial (C) aspects, and detail of the brachial articulation area in posteroventral view (D). Camera lucida drawing. Scale bar: 10 mm.

?Xichonelepis *sp., Dévonien inférieur de Qujing, Yunnan, Chine (MNHN CHD 02), plaque ventrolatérale antérieure en vue ventrale (A), dorsale (B) et médiale (C), et détail de l'articulation brachiale en vue postéroventrale (D). Dessin à la chambre claire. Échelle : 10 mm.*

ending with a small canal (scap, Fig. 7D). Clearly, this conical sheath of perichondral bone, the internal surface of which is smooth and the external surface rough, lined internally a plug of cartilage, in the same way as ascribed above to *Yunnanolepis*. The surface of the brachial articulation area bears only two faint ridges. One is anterodorsal and extends from the perichondral funnel to the prepectoral corner (adr, Fig. 7D), and may correspond in part to the parabrachial process of the Procondylolepiformes. The other one extends posteroventrally from the perichondral funnel to the ventral margin of the area (pvr, Fig. 7D), and may possibly correspond to the crescentiform ridge of the Procondylolepiformes or the ear-shaped process of *Vanchienolepis*.

We are thus in a situation where the Sinolepidae display three very different types of structure of the brachial articulation area. One (Fig. 7D) is very simple, almost comparable to that in *Yunnanolepis*, another is more complex (Figs. 1B, 5C; *Vanchienolepis*), with an incipient brachial process, and a third one (Fig. 1C, *Grenfellaspis*) is more like in the Euantiarchi, with dorsal and ventral articular fossae and a funnel pit surrounded with dermal bone. Moreover, the *Vanchienolepis*-like specimen from Qujing (Fig. 6) possesses a skull-roof which is remarkably similar to that of the Yunnanolepiformes, and quite different from that of both *Sinolepis* and the Euantiarchi. A small skull-roof from Dong Mo (TONG-DZUY & JANVIER, 1990, Fig. 14) referred with doubt to *Vanchienolepis* is also almost indistinguishable from that of the Yunnanolepiformes.

This raises the question of the monophyly of the Sinolepidae, which, to date, are characterised only by the presence of a large ventral fenestration in the thoracic armour (vfe, Figs. 6, 7) and the reduced ventral laminae of the AVL and PVL plates (LONG 1983; RITCHIE *et al.* 1992). This characteristic might be regarded plesiomorphous if the out-group for the antiarchs is the Rhenanida (GOUJET, 1984). In fact, all known rhenanids are devoid of median ventral plate and possess a large ventral space limited by the AVL plates. If the ventral fenestration is plesiomorphous, then the Sinolepidae would be non-monophyletic, and possibly paraphyletic. Conversely, the median ventral plate would have developed independently several times, since it is present in the Yunnanolepiformes, Procondylolepiformes and Euantiarchi. This question can be solved only in the framework of an extensive cladistic analysis of the Antiarcha, involving many other characters, which is beyond the scope of this paper.

EUANTIARCHI

The typical brachial articulation of the Euantiarchi comprises the helmet-shaped brachial process (brp, Figs. 1D, 5A), pierced by a median "funnel pit" (fp, Fig. 1D), and attached to the brachial recess by a pedicle, the pedal part of the process (pp, Figs. 1D, 5A). The latter separates two deep depressions or fossae, dorsal and ventral (vf, df, Figs. 1D, 5A), which accommodate the dorsal and ventral proximal central plates of the appendage respectively. In addition, there is a relatively large axillary foramen (axf, Fig. 1D). The pattern of the brachial articulation area in the Euantiarchi is quite homogeneous, but JANVIER & PAN (1982) have suggested that the anteroventral position of the pedal part of the process (the flat surface of the process facing posterodorsally) is plesiomorphous for the group, since it occurs in most of the earliest known Euantiarchi (e.g. *Hyrcanaspis* and some Asterolepidoids; Fig. 5A). This would be consistent with the hypothesis of homology in this area proposed here between *Vanchienolepis* and the Euantiarchi in this paper, in particular the resemblance between the pedal part of the brachial process in

Hyrcanaspis and the small ridge which arises ventrally to the ear-shaped process in *Vanchienolepis* (Fig. 5A, B).

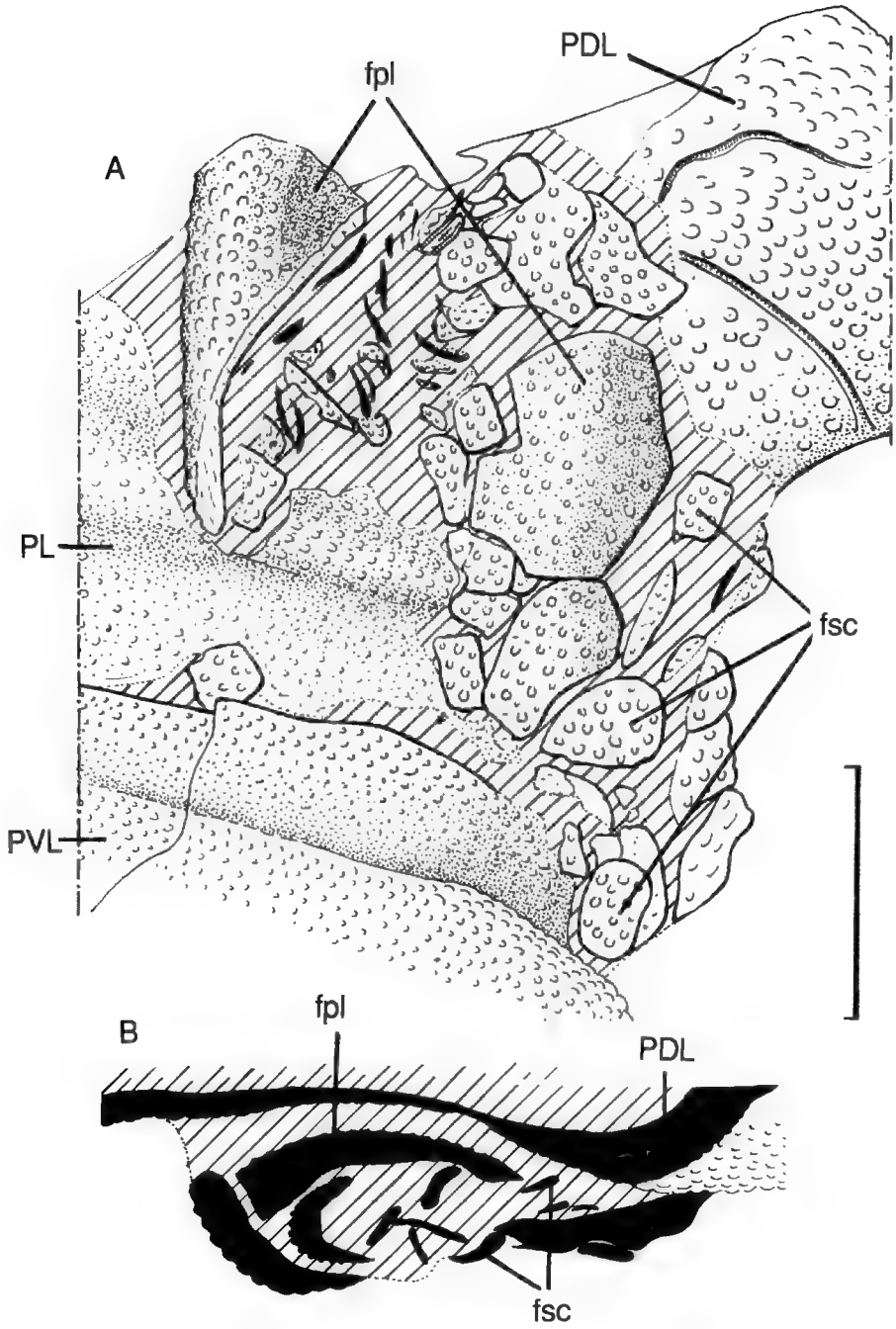
THE PECTORAL FIN

In the non-euantiarchan antiarchs the dermal covering of the pectoral fin is partly known in *Phymolepis* (referred to the Yunnanolepiformes, K.J. CHANG 1978, G. ZHANG 1978, M.M. ZHANG 1980), *Procondylolepis* (G. ZHANG 1984), *Chuchinolepis* (TONG DZUY & JANVIER, 1990), *Vanchienolepis* (or a closely related form, Fig. 6), *Sinolepis* (LIU & P'AN 1958) and *Liujiangolepis* (WANG, 1987). There is no clear evidence that the paired fins were jointed in *Phymolepis*, *Procondylolepis*, *Chuchinolepis* and *Vanchienolepis*. However, the occurrence of a fragment of a slender distal fin segment quite similar to that of *Liujiangolepis* (WANG, 1987, Fig. 1) in association with remains of *Chuchinolepis* (TONG DZUY & JANVIER, 1987, Fig. 6F) may suggest that the paired fins of the Procondylolepiformes were jointed. The pectoral fin plates of *Vanchienolepis* sp. from Qujing (Fig. 6) are quite similar to those of *Phymolepis* (G.R. ZHANG, 1978, Fig. 11; Pl. 6.9; M.M. ZHANG, 1980, Pl. 5.1), that is, polygonal and not elongated in shape. In this specimen, the proximal end of the dermal fin seems to have been made up of four plates, two centrals (Cd, Cv, Fig. 6A) and two marginals, but only three of them are actually preserved. The ventral central plate (Cv, Fig. 6A, B) abuts against the small ventral ridge (cr, Fig. 6A, B), suggested here as being homologous to the pedal ridge of euantiarchs. The other plates do not contact the AVL plate in this specimen.

In a specimen of *Yunnanolepis* sp., quite close to *Y. chii* Liu, from the Bac bun Formation of Trang Xa, Vietnam (TONG DZUY & JANVIER, 1994), an assemblage of tile-shaped platelets and minute scales are preserved against the lateral wall of the trunk armour, and may be interpreted as a pectoral fin (Fig. 8). The tile-shaped platelets look exactly like appendage plates of other antiarchs (fpl, Fig. 8A), and a transverse section of this assemblage shows that they are arranged more or less in a tube-shaped pattern (Fig. 8B). The minute scales seem to fill the gaps between the two major tile-shaped platelets, and become more and more abundant toward the rear of the specimen (fsc, Fig. 8A). This may suggest that the distal end of the pectoral fin in *Yunnanolepis* was still covered with small scales, and not with large dermal plates. It may have formed a flattened club, or a pad comparable to the paired fins of osteostracans, for example (JANVIER, 1978, Fig. 2). It cannot be ruled out, however, that this assemblage is part of the body squamation, folded along the thoracic armour, yet the larger plates do not match any of the body scales or scutes observed in these early Antiarcha.

FIG. 8. — *Yunnanolepis* sp., Early Devonian of Trang Xa, Thai Nguyên, Vietnam. Left posterolateral part of a thoracic armour associated with presumed dermal covering of the pectoral fin. A, camera lucida drawing, areas still covered with matrix obliquely hatched. B, transverse section through the upper edge of the specimen in A, matrix obliquely hatched, section of dermal bones in black (UHDG-VND70). Scale bar: 1 mm.

Yunnanolepis *sp., Dévonien inférieur de Trang Xa, Thai Nguyên, Viêt-Nam. Région postérolatérale gauche d'une cuirasse thoracique associée à la couverture dermique probable de la nageoire pectorale. A, dessin à la chambre claire, les régions non préparées sont hachurées par des traits obliques. B, coupe transversale à travers le bord supérieur du spécimen figuré en A, sédiment représenté par des hachures obliques, coupes de l'os indiquées en noir (UHDG-VND70). Échelle : 1 mm.*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DISCUSSIONS AND CONCLUSIONS

These new data on the structure of the brachial articulation in antiarchs confirm the presence of a small, perichondrally lined canal piercing the brachial recess in *Yunnanolepis*. They also confirm that the Procondylolepiformes possessed a small pectoral fenestra, filled with perichondral bone, and pierced by three minute foramina. It is thus clear that, beside the considerable reduction of the endoskeletal component of the pectoral fin articulation, there may also be a thickening of the perichondral bone of the scapulocoracoid, which makes it hardly distinguishable from the dermal bone of the AVL plate. A similar process can also be observed for example in the ptyctodontid *Chelyphorus* (MARK-KURIK, *et al.* 1991), where, in addition, the brachial articular surface is very small and almost funnel-shaped, like in early antiarchs. In contrast to the Yunnanolepiformes and Procondylolepiformes, there are considerable differences in the organization of the brachial articulation area in three genera referred to the Sinolepidae: *Vanchienolepis*, *Grenfellaspis* and the unnamed specimen described here (Fig. 7). The brachial articulation area of the AVL plate in *Vanchienolepis* displays an ear-shaped ventral lamina, or process, which is tentatively compared here to the ventrolaterally placed brachial process of supposedly primitive euantiarchs, such as *Hyrcanaspis*. This structural disparity of the Sinolepidae, as to the brachial articulation may signify that this family is not monophyletic. In this case, the large ventral fenestration of the thoracic armour, hitherto regarded as the synapomorphy of the group, would be either a symplesiomorphy for antiarchs or for the group including sinolepids and euantiarchs only, or a homoplasy in the three "sinolepid" genera. It is thus clear that any transformational approach to the structure of the brachial articular area of the Antiarcha must be considered in the framework of a phylogenetic analysis of the entire group, based also on other characteristics.

A specimen of *Yunnanolepis* sp. from the Lower Devonian of Vietnam displays what may be the distal portion of the pectoral fin, which looks as if covered with minute scales, and not large dermal plates. Although admittedly a poor evidence, this may suggest that the appendage-like structure of the antiarchan pectoral fin was not yet achieved in *Yunnanolepis*.

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Description of *Maideria falipoui* n. g., n. sp., a long snouted brachythoracid (Vertebrata, Placodermi, Arthrodira) from the Givetian of Maider (South Morocco), with a phylogenetic analysis of primitive brachythoracids

by Hervé LELIÈVRE

Abstract. — *Maideria falipoui* n. sp., n. g., a new primitive long snouted brachythoracid from the Lower or Middle Givetian of South Morocco (Presaharian Anti-Atlas) is described. The monophyletic group Migmatocephala, a taxon erected by WHITE, 1952, is redefined, together with the monophyly Eubrachythoraci. A phylogenetic analysis has been performed using PAUP program based on 53 characters coded for 12 taxa. Three equally parsimonious topologies have been found, in which *Maideria* is considered as the most primitive brachythoracid, and *Holonema* included in Eubrachythoraci.

Keywords. — *Maideria falipoui*, Givetian, Morocco, Migmatocephala, phylogenetic analysis.

Description de *Maideria falipoui* n. g., n. sp., un brachyhtoraci à museau long (Vertebrata, Placodermi, Arthrodira) du Givétien du Maider (sud marocain) et analyse phylogénétique des brachythoraci primitifs

Résumé. — *Maideria*, un nouveau genre de brachythoraci du Dévonien moyen (Givétien inférieur ou moyen) du Maider, Anti-Atlas présaharien, est décrit. Une analyse phylogénétique informatisée des relations de parenté entre les brachythoraci primitifs (Migmatocephala) et les Eubrachythoraci, conduite à l'aide du logiciel de parcimonie PAUP, a permis d'isoler trois topologies également parcimonieuses. Dans l'arbre consensus trois groupes monophylétiques sont définis. Le taxon supragénérique monophylétique, Migmatocephala, créé par WHITE, 1952 est utilisé pour regrouper un ensemble de genres autrefois associés au sein des brachythoraci primitifs. *Maideria falipoui* représente le taxon le plus primitif des brachythoraci, et le genre *Holonema* est placé au sein des Eubrachythoraci.

Mots-clés. — *Maideria falipoui*, Givétien, Maroc, Migmatocephala, analyse phylogénétique.

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INTRODUCTION

Devonian Moroccan fish faunas are best known from the Upper Devonian layers of Tafilalt (LEHMAN, 1956, 1976, 1977, 1978; LELIÈVRE, 1991) where, mostly, giant placoderms have been described, together with the remains of an eusthenopterid (LEHMAN, 1978; LELIÈVRE & JANVIER, 1986), and some isolated fragments of sarcopterygians of which some has been referred to cœlacanthids (LELIÈVRE & JANVIER, 1988). The more westerly situated Devonian Maider Basin has not been so extensively investigated. LEHMAN (1976) mentioned the occurrence of isolated

placoderm remains in the Frasnian, Northwest of Fezzou. He figured two incomplete median dorsal plates of the poorly known genus *Aspidichthys* (LEHMAN, 1976; Pl. 9, Figs. C, D), and some thoracic dermal plates of *Holonema* (LEHMAN, 1977; Pl. 3, Fig. F). Recently, I have collected remains of selenosteids, and isolated *Ctenacanthus* spines in the same area in the Frasnian of the Jbel Issoumour.

The type specimen of *Maideria* described below has been generously given to the Muséum national d'Histoire naturelle by M. Christian FALIPOU, who purchased it in one of the numerous fossils shops of this area of South Morocco. The type material comes from somewhere in the Maider, although the precise locality remains unknown. The other specimens MCD 186, 187, 191 come from either the Jbel Issoumour or the Jbel Merakib, respectively in the North and in the South of Maider. All the specimens were excellently preserved in a marine limestone which contains conodonts, indicating a lower or middle givetian age.

In the same sections of the Givetian of the Maider other fish remains have been found in association with *Maideria*. They compose a new Middle Devonian fish fauna in which various taxa have been identified: an eastmanosteid represented by a left dorsolateral plate, left and right anterior ventrolateral plates belonging to a different eubrachythoracid genus new petalichthyids represented by incompletely preserved skull-roofs, an inferognathal plate of a ptyctodontid referred to *Paleomylus*, and microvertebrates remains, mainly scales of acanthodians and chondrichthyans. Finally, and for the first time in the Devonian of Africa, a dipnoan palate was found. The description of the entire fauna will be given in a forthcoming paper.

ABBREVIATIONS

ADL cf.	anterior dorsolateral contact surface, *surface de contact pour la plaque ADL*;
AL	anterior lateral plate, *plaque antérolatérale*;
a.pr	antorbital dermal process, *processus dermique antéorbitaire*;
ASG	anterior superognathal, *superognathal antérieur*;
a.tr	anterior teeth row, *rangée de dents antérieures*;
AVL	anterior ventrolateral plate, *plaque ventrolatérale antérieure*;
cf.PVL	posterior ventrolateral contact surface, *surface de contact pour la plaque PVL*;
C	central plate, *plaque centrale*;
cr.inf	inframarginal crista, *crête inframarginale*;
cr.pb	postbranchial crista, *crête postbranchiale*;
cr.po.	postorbital crista, *crête postorbitaire*;
cr.pr	carinal process, *processus carinal*;
csc	central sensory line, *sillon sensoriel central*;
d.end.e	external endolymphatic duct, *ouverture externe du ductus endolymphatique*;
d.end.i	internal endolymphatic duct, *ouverture interne du ductus endolymphatique*;
dp.m cu	cucularis depression, *dépression cucculaire*;
d.pro.pr	dermal preorbital process, *processus dermique préorbitaire*;
end. fi	endocranial fissure, *fissure endocrânienne*;
f.pi	pineal fossa, *fossette pinéale*;
fo.hy	hyoid muscle fossa, *fosse pour le muscle hyoïde*;

IL cf	interolateral contact face, *surface de contact pour la plaque IL*;
IN	internasal plate, *plaque internasale*;
ioc.ot	otic branch of infraorbital sensory line, *branche otique de la ligne sensorielle infraobitaire*;
ioc.pt	postorbital branch of infraorbital sensory line, *branche postorbitaire de la ligne sensorielle infraorbitaire*;
laf	lateral articular fossa, *fosse articulaire latérale*;
lc	main lateral sensory line, *ligne sensorielle principale*;
l.iob	infraobstantic lamina, *lame infraobstantique*;
l.tr	lateral teeth row, *rangée de dents latérales*;
M	marginal plate, *plaque marginale*;
MD	median dorsal plate, *plaque médiane dorsale*;
mp	middle pit-line, *pit-line moyenne*;
n.cap	nasal capsule, *capsule nasale*;
nn	nasal notch, *encoche nasale*;
Nu	nuchal plate, *plaque nuchale*;
?o.a. PN	contact face for postnasal plates, *contact pour les plaques postnasales*;
occ	occipital sensory line cross-commissure, *commissure sensorielle occipitale*;
orb	orbit, *orbite*;
P	pineal plate, *plaque pinéale*;
PDL cf	posterior dorsolateral plate contact surface, *surface de contact pour la plaque PDL*;
PM	postmarginal plate, *plaque postmarginale*;
PN oa	overlapped area for postnasal plate, *aire de contact pour la plaque postnasale*;
PNu	paranuchal plate, *plaque paranuchale*;
PrO	preorbital plate, *plaque préorbitaire*;
PtO	postorbital plate, *plaque postorbitaire*;
pap	para-articular process, *processus para-articulaire*;
pbe	postbranchial embayment, *incision postbranchiale*;
p.emb	pectoral embayment, *incision pectorale*;
pmc	postmarginal sensory line, *ligne sensorielle postmarginale*;
pn.p	postnuchal process, *processus postnuchal*;
pp.	posterior pit-line, *pit-line postérieure*;
p.pr	posterior process of nuchal plate, *processus postérieur de la plaque nuchale*;
p.pt	pineal pit, *fossette pinéale*;
pr.apo	anterior postorbital process, *processus antérieur postorbitaire*;
pr. ect	ectethmoid process, *processus ectethmoïde*;
pr.in	internasal process, *processus internasal*;
pr. m	medial process of anterolateral plate, *processus médial de la plaque antérolatérale*;
pr. ob	obstantic process, *processus obstantique*;
pr.ppo	posterior postorbital process, *processus postorbitaire postérieur*;
pr.so	supraorbital process, *processus supraorbitaire*;

pt.pr.	posterior median process of nuchal plate, *processus postéromédian de la plaque nuchale*;
R	rostral plate, *plaque rostrale*;
SM	submarginal plate, *plaque submarginale*;
SO cf	suborbital plate contact surface, *surface de contact pour la plaque suborbitaire*;
Sp m	spinal margin, *bord spinal*;
soa	subobstantic area of skull-roof, *aire subobstantique du toit crânien*;
soc	supraorbital sensory line, *ligne sensorielle supraorbitaire*;
suo.v	supraorbital vault, *voûte supraorbitaire*;
svg.f	supravagal fossa, *fosse supravagale*;
th.pre	pre-endolymphatic thickening, *épaississement pré-endolymphatique*;
vts	transverse ventral sensory line, *ligne sensorielle ventrale.*

SYSTEMATIC PALAEONTOLOGY

Ordre ARTHRODIRA Woodward, 1891a
Family indet.
Genus **MAIDERIA** n. g.

ETYMOLOGY. — from Maider, an Arabic name which means the place where the trees grow without water.

DIAGNOSIS. — A brachythoracid with a long closed and upturned snout composed of the rostral and, ventrally, by a broad internasal plate.

REMARKS. — Potential autapomorphies might be included in the definition, as for instance the posterior median process of the anterior lateral plate (MCD 187), when similar material will be found associated with characteristic plates of *Maideria*.

TYPE-LOCALITY. — Maider Basin, exact locality unknown.

TYPE-LEVEL. — Lower or Middle Givetian.

Maideria falipoui n. g., n. sp.
(Figs. 1-12)

TYPE-SPECIES. — *Maideria falipoui* n. sp.

ETYMOLOGY. — After Christian FALIPOU who gave the specimen to the Muséum national d'Histoire naturelle, Paris.

DIAGNOSIS. — The same as for the genus, by monotypy.

HOLOTYPE. — Collection number: MCD 184, an almost complete skull-roof with the left anterior superognathal in anatomical position.

OTHER MATERIAL. — It includes an anterior and fragmentary part of a rostral plate, associated with an almost complete right anterior ventrolateral plate (MCD 190).

Recently, new material of *Maideria* has been given by C. FALIPOU to the Muséum national d'Histoire naturelle. It comes from both the Northern (Jbel Issoumour) and Southern (Jbel Mer-

akib) parts of the Maider. This material is composed of an almost complete skull-roof (MCD 191), an isolated median dorsal plate (MCD 186), and a right anterior lateral plate (MCD 187). Although MCD 186, 187 were not associated with typical material belonging to *Maideria*, these two plates are referred to this form according to their dermal ornamentation which consists of tubercles, sometimes aligned in rows.

All this material has been chemically prepared using a solution of formic acid diluted at 10%. Phosphatic microremains were collected and belong to vertebrates (see below) and conodonts which were identified by P. BULTYNCK (Brussels) as:

Polygnathus linguiformis linguiformis Hinde, 1879
Polygnathus hemiansatus Bultynck, 1987.

The latter species is well known in different, but successive conodont zones: *P. ensensis*, *P. timorensis* and *P. varcus*, distributed from the Lower Givetian to the Middle Givetian respectively. No other typical invertebrate was associated, therefore it is still impossible to know the precise stratigraphical level where *Maideria* comes from. Isolated acanthodian scales of the *Cheiracanthoides*-type, acanthodids with an unornamented crown, *Cladolepis* type scales, and isolated platelets of rhenanid type with pointed tubercles have been collected from the same sample. All these microremains are badly preserved, abraded and black-coloured, indicating that they have been submitted to heat.

DESCRIPTION

The type-specimen is an almost complete skull-roof with most of the snout preserved, and with only its right posterolateral corner missing. No cheek plate is known, but the left anterior superognathal is completely preserved. The thoracic armour is represented by a right anterior ventrolateral, a median dorsal and a right anterior lateral plate which are tentatively referred to *Maideria* on the ground of their ornamentation.

The overall shape of the type skull-roof is longer than broad, and strongly arched transversely (Figs. 2, 7). The estimated breadth/length index is 86%, a ratio which makes it nearer to the proportions in *Eastmanosteus calliaspis* (87,2%, in DENNIS-BRYAN, 1987) than to long-snouted brachythoracids from Gogo (*Camuropiscis concinnus*, 48%; *Rolfosteus*, 31,7%; *Latocamurus*, 65%). Typical coccosteids such as *Coccosteus cuspidatus* (140-148%) have a broader skull-roof. The orbits are relatively large, deep and face laterally. The snout is broad and strongly upturned. The ornamentation is composed of tubercles with both stellate and non-stellate bases. These are small and rounded, equal in size, except those from the tip to the ventral margin of the rostrum, which are larger, closely-set and more or less regularly arranged in rows. The same pattern is found on a narrow strip bordering the dorsal medial margin of the orbit, where the tubercles are smaller and regularly spaced.

No suture is visible on the dorsal surface of the type-specimen (Figs. 1, 7), but some could be located on radiographs (Fig. 2). This condition is not exclusive to *Maideria*, and it has been also mentioned for *Buchanosteus* (GARDINER & MILES, 1990: 190; WHITE & TOOMBS, 1972, Pl. 2, Fig. 3). The second skull-roof (MCD 191) is of almost same size, but shows the sutures

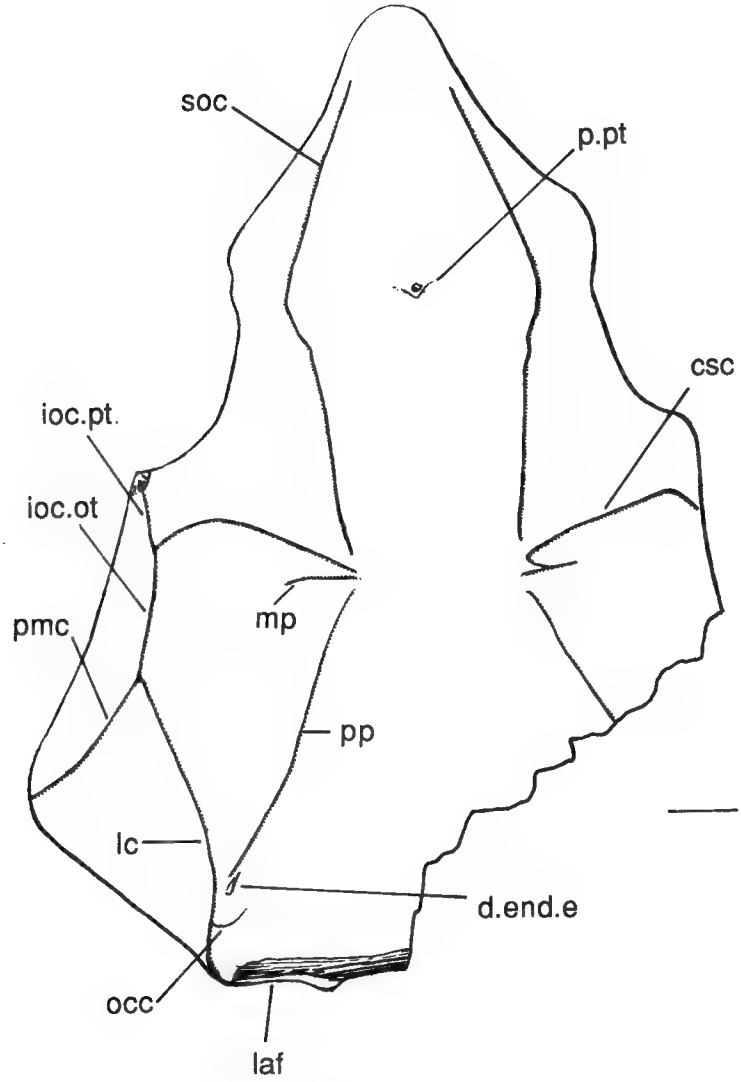


FIG. 1. — *Maideria falipoui* n. g., n. sp. Holotype specimen MCD 184. Dorsal view of the skull-roof. Scale bar: 1 cm.
Maideria falipoui *n. g., n. sp. Holotype MCD 184. Vue dorsale du toit crânien. Échelle : 1 cm.*

(Fig. 3). The attempted reconstructions of the skull-roof in dorsal, ventral and lateral views (Figs. 9, 10) are combined from both specimens (MCD 184 and 191).

The ventral surface of the skull-roof does not exhibit any well-defined dermal structures, and those which are usually described in eubrachythoracids are apparently absent in *Maideria*, which thus retains a plesiomorphic condition.

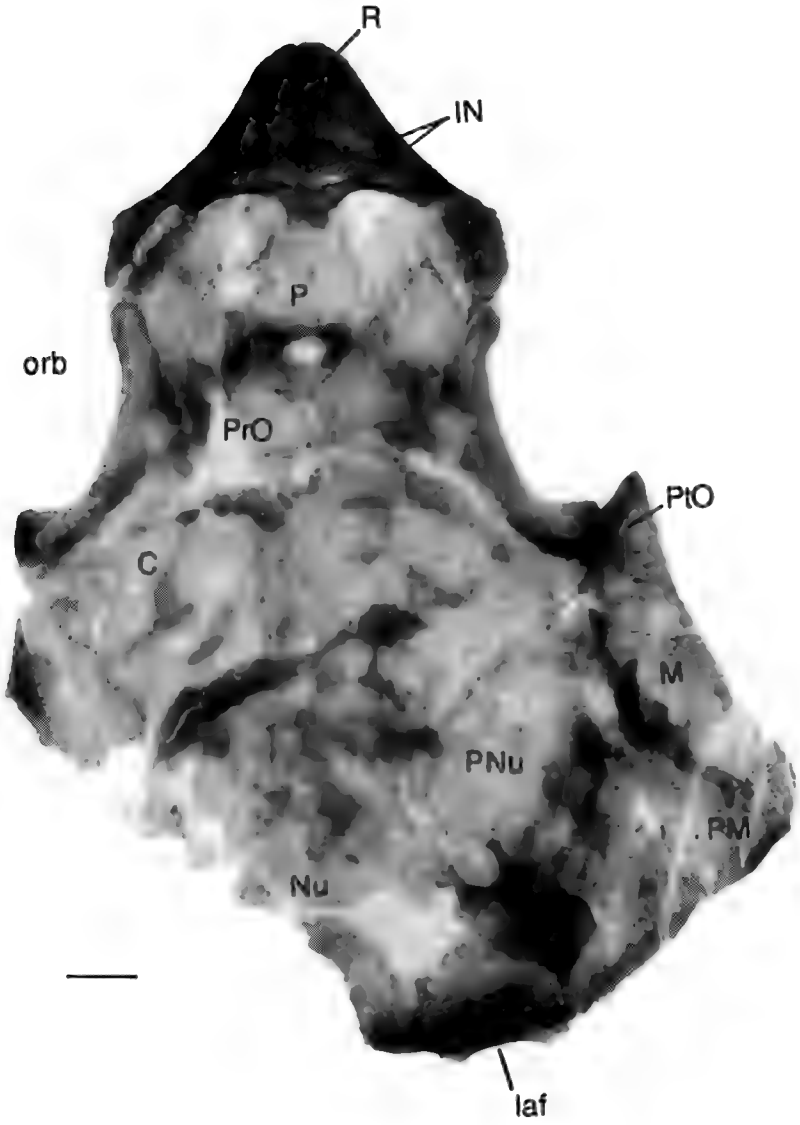


FIG. 2. — *Maideria falipoui* n. g., n. sp. Holotype specimen MCD 184. Radiograph of the skull-roof. Scale bar: 1 cm.
Maideria falipoui *n. g., n. sp. Holotype MCD 184. Radiographie du tout crânien. Échelle : 1 cm.*

Some measurements of the skull-roof are given, following the standard series of MILES & DENNIS (1979, Figs. 1, 2, 3).

Length of skull in the midline, approximately	MCD 184	14,4 cm
Skull breadth across the	MCD 184	12,4 cm
posterolateral angles, approximately	MCD 191	13 cm
Prepineal length of skull	MCD 184	4,5 cm
Length of the fenestra orbitalis	MCD 184	4,5 cm
Length of the nuchal plate	MCD 184	5,3 cm
in the midline	MCD 191	5,2 cm
Breadth of the articular fossa	MCD 184	1,7 cm
	MCD 191	1,9 cm
Length of postorbital division of the cheek	MCD 184	5,6 cm
	MCD 191	6,4 cm

Nuchal plate (Nu)

This plate is almost entirely preserved, and its posterior medial margin is shown in MCD 191. It is relatively short, and represents approximately 37% of the skull-roof length. Its shape is almost trapezoid, and the anterior suture is straight in dorsal view, and convex in ventral view (Figs. 8D, 5).

Its visceral face is flat, and a shallow medial depression extends anteriorly to the presumed position of the poorly developed posterior process (pt.pr, Fig. 9). The posterior medial region is not preserved in the holotype, and badly preserved in MCD 191, and I cannot affirm that the two small, medially placed, posteriorly opening depressions correspond to the nuchal pits (Fig. 8D). Nevertheless, I assume that they did not open ventrally, the problem being to know whether they opened dorsally or posteriorly. These last two possibilities are considered plesiomorphic, and close to the dolichothoracid condition (e.g. *Dicksonosteus*, GOUJET, 1984, Fig. 31). There is no posterior nuchal thickening (Fig. 8B), as usually seen in primitive brachythoracids (see LELIÈVRE *et al.*, 1990: 60-61). The lateral part of this thickening is only developed in connection with the lateral position of the articular fossa (laf). In comparison with typical primitive brachythoracids, as defined by LELIÈVRE (1984a, b; 1988), the nuchal plate is short, and its general shape and proportions suggest the condition met with in eubrachythoracid skull-roofs.

Paranuchal plate (PNu)

The left plate is well preserved in both skull-roofs (MCD 184, 191). The almost straight anterior margin is in contact with the postorbital plate, thereby separating the central from the marginal plates, a condition which probably evolved several times in placoderms. There is a distinct posterior lobe, well defined in MCD 191 (Fig. 3), but not clearly distinguishable in the radiograph (Fig. 2). The suture between the paranuchal and the marginal plates runs parallel to the postmarginal sensory line (pmc), a disposition shared with *Antineosteus* (LELIÈVRE, 1984b, Fig. 1), *Buchanosteus* (YOUNG, 1979, Fig. 1) and *Taemasosteus novaustrocambricus* (WHITE, 1978, Fig. 112). A postnuchal process (pn.p) is well defined in MCD 191 (Figs. 3, 9). The subobstantic skull-roof area (soa) is very long (due to the strong posterior curvature of the skull-

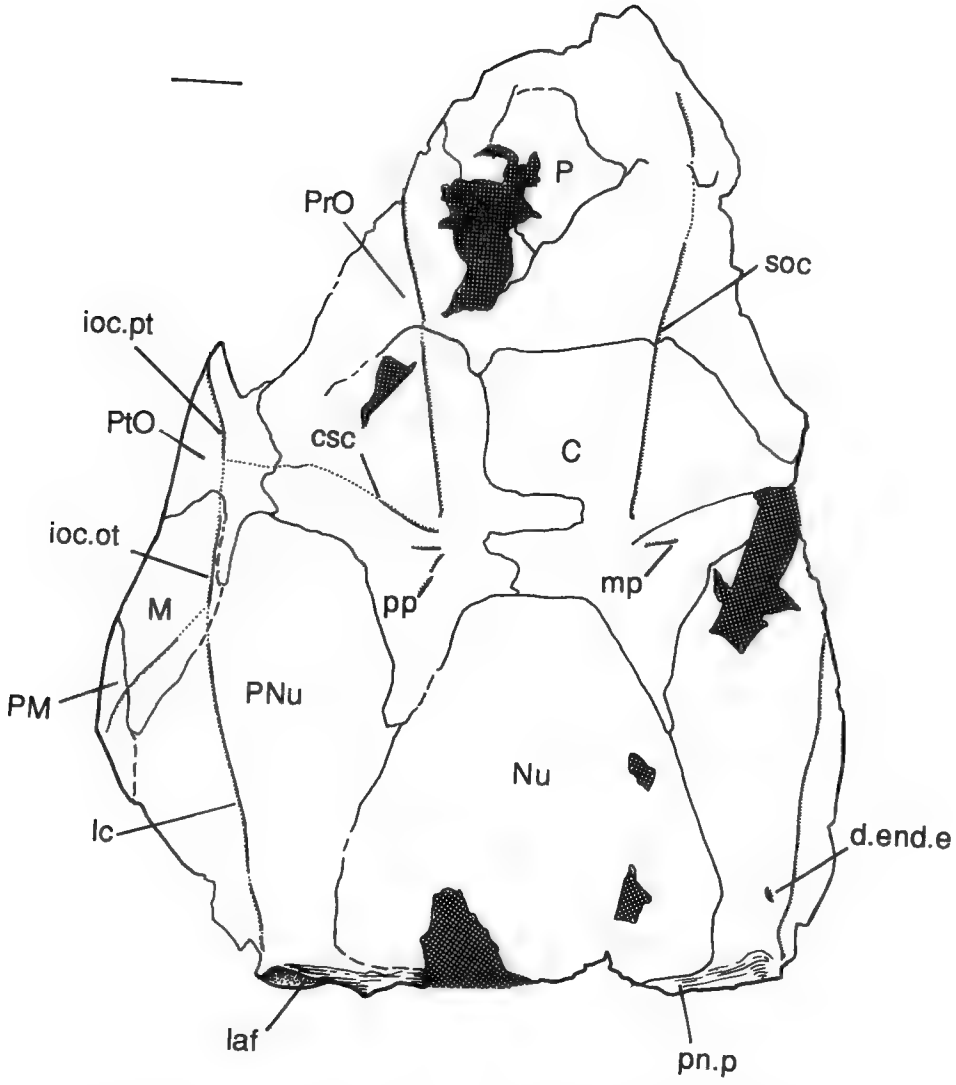


FIG. 3. — *Maideria falipoui* n. g., n. sp. Skull-roof in dorsal view, MCD 191. Scale bar: 1 cm.
Maideria falipoui *n. g., n. sp. spécimen MCD 191. Vue dorsale du toit crânien. Échelle : 1 cm.*

roof), but the extension of the contact with the thoracic armour is small (Fig. 10). The dorsal surface is grooved by three sensory lines: the main lateral sensory line (lc), the posterior pit-line (pp), which does not contact posteriorly the main lateral line in the holotype, and the occipital commissure (occ). The external opening of the endolymphatic duct (d.end.e) is elongated, and more anteriorly placed than is usual in brachythoracids.

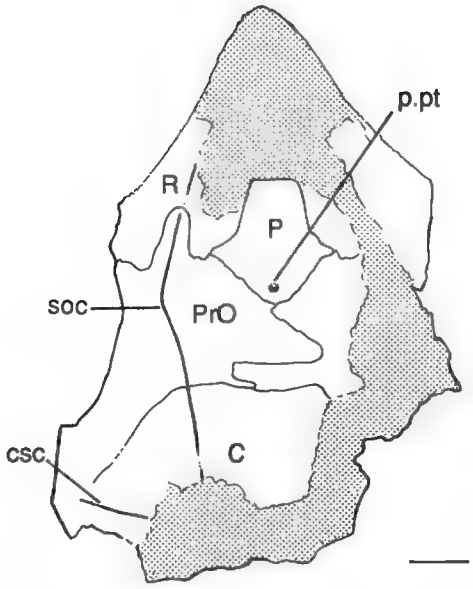


FIG. 4. — *Maideria falipoui* n. g., n. sp. Partly preserved anterior part of a skull-roof MCD 197. Dorsal view. Scale bar: 1 cm.

Maideria falipoui *n. g., n. sp. Vue dorsale de la région antérieure du toit crânien MCD 197. Échelle : 1 cm.*

The lateral articular fossa (laf) is well preserved, but is small in comparison with the typical primitive brachythoracid condition where this fossa is enlarged and higher medially than laterally. The pararticular process (pap, Figs. 5, 10) is reduced, and situated below the posterior skull-roof margin. It is usually well developed in primitive brachythoracids and projects beyond the posterior margin of the skull-roof. On the ventral surface, the cuccularis depression (dp.m cu, Fig. 5) is shallow, and its anterior limits are clearly delineated by a small ridge which represents a remnant of the neurocranial walls in both MCD 184 and 191. The endolymphatic duct (d.end.i) is slightly developed as a depressed tube. Its anterior position is the same as in *Buchanosteus* (YOUNG, 1979, Fig. 2), but there is no such a long perichondral tube as seen in *Antineosteus* (LELIÈVRE, 1984a, Pl. 3c). The latter condition is considered as correlated with a long posterior part of the skull-roof (LELIÈVRE, 1984b). Posteriorly, the supravagal fossa (svg.f) is preserved together with a small part of the endocranium which bears the two posteriormost openings for the spino-occipital nerves.

Postmarginal plate (PM)

The left plate is preserved in both skull-roofs and does not have the usual triangular shape. Its anterior margin is sinuous, and its surface is grooved by the postmarginal sensory line (pmc, Figs. 1, 9, 10).

The visceral surface bears a low crest which is the distal part of the inframarginal crista (cr.inf, Fig. 5).

Marginal plate (M)

The left plate is completely preserved in both specimens MCD 184, 191. It is in contact with the postorbital, paranuchal, and postmarginal plates (Figs. 3, 9, 10). There is no contact

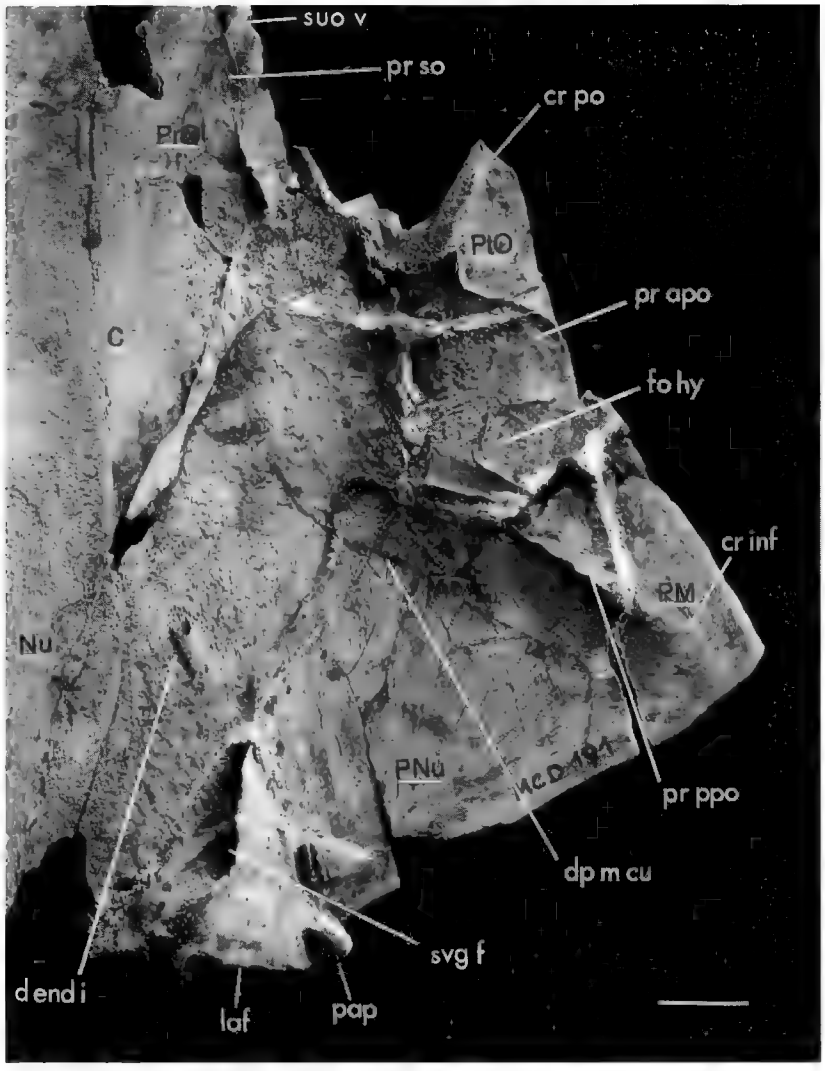


FIG. 5. — *Maideria falipoui* n. g., n. sp. Specimen MCD 191, ventral view of the left side. Scale bar: 1 cm.
Maideria falipoui *n. g., n. sp. Spécimen MCD 191, vue ventrale du côté gauche. Échelle : 1 cm.*

with the central plate, a condition which occurs in different species of *Holonema*, but also in some Eubrachythoraci. Contrary to the elongate marginal plate of typical primitive brachythoracids (e.g. *Homostius*, *Antineosteus*, *Arenipiscis*, *Buchanosteus*) this bone is only slightly longer than broad.

The visceral surface shows a well preserved inframarginal crista (cr.inf), an extension of the endocranial postorbital process (pr.ppo; Fig. 5). This crista is low and slightly sinuous, re-

calling that of *Buchanosteus* (YOUNG, 1979, Fig. 2). The margins of this crista run almost parallel, and a small oval depression is seen at the distal end of its groove in the holotype. The anterior margin of the groove turns anteriorly to reach the lateral margin of the skull-roof, contrary to what is seen in *Buchanosteus*, and isolates a small area which corresponds to the hyoid muscle fossa of *Buchanosteus* (fo.hy; YOUNG, 1979, Fig. 2).

Three sensory lines occur on the marginal plate: the postmarginal sensory line (pmc), a short part of the main lateral line, and the otic branch of infraorbital sensory line (ioc.ot). The course of the latter is parallel to the suture between the marginal and paranuchal plates, and situated medially, a disposition shared with primitive brachythoracids and regarded as a synapomorphy (character 2, *in* LELIÈVRE, 1988, Fig. 4), even if the marginal plate remains short.

Postorbital plate (PtO)

This plate is a relatively small component of the skull-roof and its lateral margin forms the posterior part of the dorsal orbital margin (Figs. 3, 9). It is in contact with the preorbital, central, paranuchal and marginal plates and lacks the lateral elongated process of *Taemasosteus* (WHITE, 1978, Fig. 82) or *Arenipiscis* (YOUNG, 1981, Fig. 9). The length of the lateral margin represents less than half of the lateral skull-roof margin. A long and slender posterior process separates the anterior part of the marginal and paranuchal plates (Fig. 9).

The visceral surface exhibits the most conspicuous structures of the skull-roof. Anteriorly to the hyoid muscle fossa, a ridge of perichondral bone, runs from the lateral margin of the skull-roof and makes a sharp angle to join the posterior dermal supraorbital crista, or postorbital crista (cr.po; see also CARR, 1991: 380). The area situated between the anterior part of the hyoid muscle fossa and the posterior region of the postorbital crista corresponds to the anterior postorbital process (pr.apo) of *Buchanosteus*. The shallow supraorbital vault (suo.v) is embayed for the supraorbital process (pr.so; Figs. 5, 6), and is bounded off posteriorly by the postorbital crista, which may be considered as the only developed portion of the lateral consolidated part (Fig. 5). There is no triangular depression, as in camuropiscids (tri; DENNIS & MILES, 1979b, Fig. 16).

There is no distinct dorsal overlap area for the contact with the suborbital plate. The dermal postorbital process is well defined and probably had a posterior contact area with the suborbital plate, which was loosely attached to the skull-roof, unlike the condition in the camuropiscids (DENNIS & MILES, 1979b, Fig. 3).

Central plates (C)

Both plates are entirely preserved in the holotype and show an asymmetrical development, the left one being broader than the right one (Fig. 2), a condition which occurs also in *Antineosteus*. MCD 191 (Fig. 3), shows the opposite asymmetry. Their median suture is almost straight in the holotype and sinuous in MCD 191. There is no contact with the pineal plate, as in most primitive brachythoracids, except *Homostius* (HEINTZ, 1934, Fig. 1). Usually, this contact occurs in eubrachythoracids, where the pineal protrudes between the anterior margin of the centrals. The general shape of the central plate, without any anterior or lateral lobe, is typical for primitive brachythoracids and is probably linked with the separation from the pineal plate by the preorbital plates. The visceral surface is flat, and the pre-endolymphatic thickening is lacking.

The sensory lines are normally developed, with the supraorbital (soc), and the central sensory lines (csc), which are both separated. The middle (mp) and posterior pit-lines (pp), are present and the latter shows a peculiar pattern on the right side of the holotype (Fig. 1).

Preorbital plate (PrO)

The preorbitals have a postpineal contact, and their median suture is sinuous (Fig. 4). The lateral margin forms more than half of the dorsal orbital margin, but the dermal anteorbital process (a. pr), is apparently formed by the rostral plate, or an expansion of the postnasals, but this cannot be checked.

The visceral surface shows no contact area for the attachment of the suborbital lamina of the suborbital plate. Accordingly, its medial margin is grooved for a contact with the postnasal plate (?oa, PN, Fig. 6B). It is probably this latter plate which establishes ventrally the contact with the suborbital plate, as it may also be indicated by the ventrolateral position of the nostrils (nn, Fig. 6A). This suggests that the postnasal plates probably participated to the ventral anterior margin of the orbit, in a pattern which is similar to that in camuropiscids, but also to such dolichothoracids as *Dicksonosteus* (GOUJET, 1984, Figs. 3B, 50). Considering the definition of the camuropiscids given by LONG (1988: 235), "...the postnasal plates large, excluding contact between the suborbital and preorbital plates..." does not appear to be a synapomorphy of the camuropiscids (see also LONG, 1990), since it is also met within dolichothoracid, which has anteriorly placed orbits, and probably also within *Maideria*.

The supraorbital vault is almost flat (suo.v), except in its posterior part where it thickens to form the anterior part of the postorbital crista. Its medial margin is clearly limited by remnants of perichondral bone of the endocranial wall. In the middle part of the dorsal orbital margin, a projection of the perichondral bone indicates the position of the endocranial supraorbital process (pr.so), which lies more posteriorly than in *Buchanosteus* (YOUNG, 1979, Fig. 2). The perichondral bone is preserved anteriorly on both sides, with the left side better preserved in the holotype. This region shows the lateral part of the rhino-ethmoidian fissure (end. fi; Fig. 10), which opened between the rostral capsule and the anterior part of the endocranium in the ectethmoid region. The left anterior superognathal (ASG) is still attached to the ectethmoid endocranial process (pr.ect; Figs. 6B, 10). Its occurrence is known in *Buchanosteus* and certains Spitsbergen dolichothoracids such as *Dicksonosteus* (GOUJET, 1984, Fig. 8A).

REMARKS: Recently MILES & GARDINER (1990: 194) argued for the absence of the ethmoid fissure, with a perichondral continuity between the ethmoid part of the neurocranium and the rostral capsule in placoderms. In this, they contradicted the observations of YOUNG (1979, 1986), and overlooked the data published by GOUJET (1984) on Spitsbergen dolichothoracids. In both *Buchanosteus* and some taxa from Spitsbergen, the presence of this fissure is clear. GOUJET (1984: 231-233; Fig. 8) defined three different conditions of this fissure among arthrodires. *Buchanosteus* and some dolichothoracids share the same disposition: an open fissure, with a rostral capsule covered dermally by the rostral and the pineal plates, and sometimes by the postnasal plates. The pineal plate may be broad with its lateral margin reaching the dorsal orbital margin, and its posterior margin coinciding with the ethmoid fissure. This explains why the two parts of the skull-roof are often found separated (YOUNG, 1979, Pl. 1A, B; GOUJET, 1984: 232).

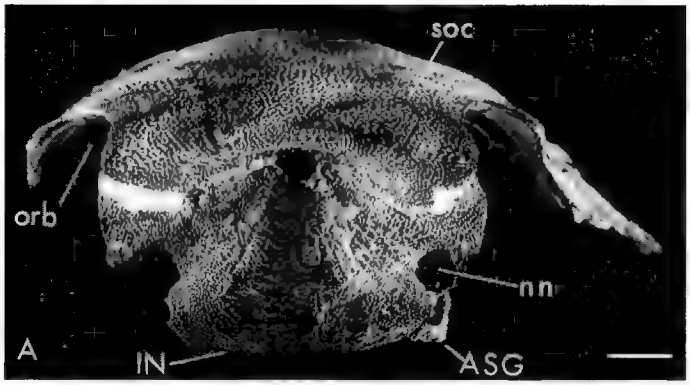
The cranial fissure of *Maideria* can be considered to belong to the second type defined by GOUJET (1984), where the ethmoid region is complete and forms anteriorly a transverse internal septum (see STENSIÖ, 1963, Figs. 52A-D). The fusion between both endocranial structures is reinforced dorsally by either a broader pineal plate, a process of the preorbital plate, or both. This condition is found in certain arctolepids (*Lehmanosteus*, *Dicksonosteus*, *Heintzosteus*, see GOUJET, 1984).

The internal transverse septum between the two ossifications is only partly preserved in *Maideria*, and so does not allow to conclude as to the condition of the structure in this taxon. The pineal is relatively well developed and its lateral margins do not reach the orbit. It is large and dermally reinforcing the rhino-ethmoidian fissure, as probably did the preorbital plates with their developed medial suture, a condition which occurs in most of the primitive brachythoracids (*Antineosteus*, *Buchanosteus*, *Arenipiscis*, *Errolosteus*).

Other data on the endocranial ethmoid region of brachythoracids are provided by some Gogo species: *Rolfosteus* (DENNIS & MILES, 1979a), *Incisoscutum* (DENNIS & MILES, 1981), *Eastmanosteus calliaspis* (DENNIS-BRYAN, 1987), and recently *Latocamurus* (LONG, 1988). None of these clearly shows an open rhino-ethmoidian fissure, but the well preserved ethmoidian region of *Latocamurus* (LONG, 1988, Figs. 10, 12) may well fit in the second of GOUJET's types, where both ossifications are tightly fused, and where the rostral capsule is reduced to the nasal capsules. The remaining part of the rhino-ethmoidian fissure is represented by perichondral trabecles enclosing a blood vascular plexus. However, it seems that in eubrachythoracids the rostral region is shortened, even in long-snouted Gogo genera, since the nasal capsules bear a more dorsal position and are more closely set. The structure of the ethmoidian part of the endocranium in *Latocamurus* is reminiscent of what STENSIÖ (1963) described in *Tapinosteus* (STENSIÖ, 1963, Fig. 52A-B) or *Pholidosteus* (STENSIÖ, 1963, Figs. 51C, 75), except for the anteriormost part of the endocranium, which is reconstructed. I consider both *Tapinosteus* and *Pholidosteus*, together with *Latocamurus*, as belonging to the same second type retained by GOUJET (1984). *Trematosteus fontanellus* (STENSIÖ, 1963, Figs. 91B, C), which has been considered by GOUJET (1984: 233) as being a possible representative of a third type, does not, in my opinion, show a marked difference from the condition observed in *Tapinosteus* or *Pholidosteus*. Even less is known about the dorsal rostral ossification of *Trematosteus*.

Another brachythoracid ethmoidian structure is represented by both species of *Torosteus* (GARDINER & MILES, 1990, Figs. 14, 15, 29), *Eastmanosteus calliaspis* (DENNIS-BRYAN, 1987, Fig. 16A-C), or *Dunkleosteus marsaisi* (pers. obs. on Moroccan material), where the ethmoidian ossification is probably cartilaginous, except for the well-defined ectethmoid process (DENNIS-BRYAN, 1987, Figs. 15C, D). Nevertheless, a new structure occurs, where the nasal capsules are strongly ossified and shaped into cupules pierced by numerous foramina for the fila olfactoria. Posteriorly, the cupules are opened by a short canal for the olfactory tract (GARDINER & MILES, 1990, Fig. 29).

Finally, YOUNG's proposal (1986: 20), that the division between the rostral capsule and the remaining part of the endocranium, and the separation of the nasal capsules, are placoderm symplesiomorphies sound likely. However, the condition of the nasal capsule in *Petromyzon* ('where the nasal capsules are attached to the braincase by connective tissue'), argued for by YOUNG in his proposal, does not seem to orientate this character. Even if it seems obvious that the per-



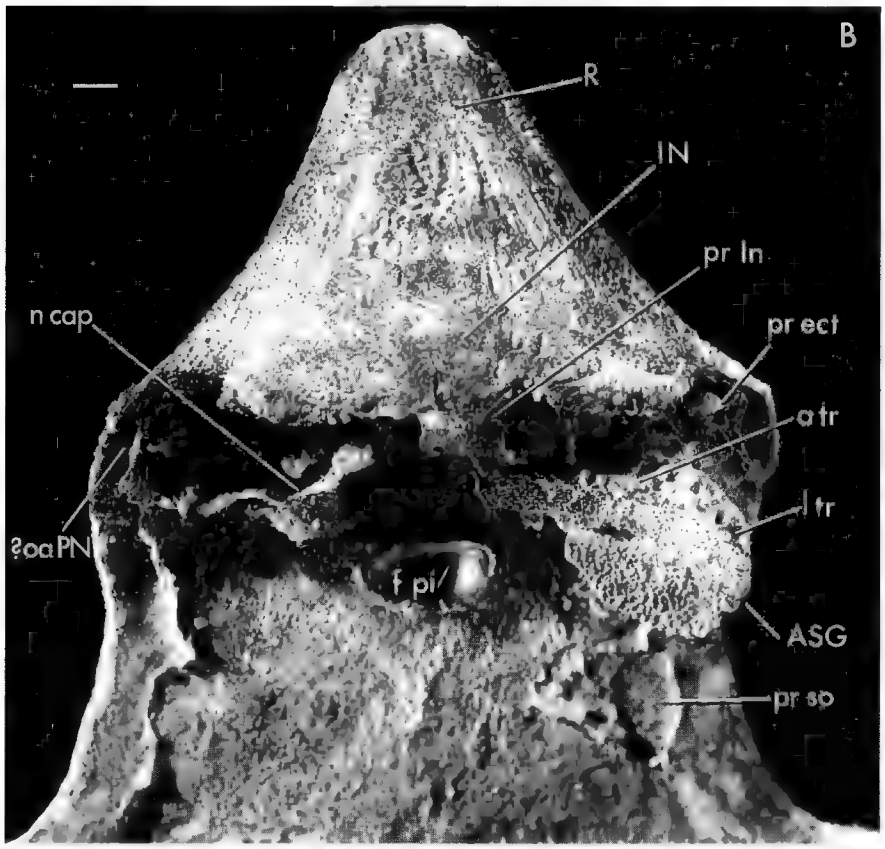


FIG. 6. — *Maideria falipoui* n. g., n. sp. Holotype specimen MCD 184. A, anterior view. B, ventral view of the anterior part of the skull-roof. Scale bar: 1 cm.

Maideria falipoui *n. g., n. sp., Holotype MCD 184. A, vue antérieure. B, vue ventrale de la région antérieure du toit crânien. Échelle : 1 cm.*

sistence of this fissure in placoderms can be interpreted as plesiomorphic, its closure or replacement by a blood vascular plexus is also a tendency reinforcing YOUNG's interpretation of this fissure as a plesiomorphic condition.

Pineal plate (P)

This bone is longer than broad, with a relatively well developed dorsal surface. Its anterior margin is placed anteriorly to the orbits. It is in contact with the preorbital and rostral plates (Figs. 3, 4, 9).

Ventrally, the pineal fossa (f.pi; Fig. 6B) is deep, and broader than long, a small posteriorly situated ridge thickens the surface and could be considered either as the probable position of the cerebral vein, or also as the dorsal position of the rhino-ethmoidian fissure.

Rostral plate (R)

This plate is a well-developed bone, triangular in shape in dorsal view, with a large ventral lamina which ends in a straight margin, giving *Maideria* an elongate, closed snout (Figs. 2, 6, 10). Laterally, the rostral plate is produced into the dermal antorbital process (a.pr), which forms the anterior part of the dorsal margin of the orbit. Its anterior position gives the orbit an elongated shape, with an inclined anterior descending margin (Figs. 6A, 10). The rostral plate is in contact posteriorly with the pineal and preorbital plates. The supraorbital sensory line (soc) is present on the lateral parts of the dorsal surface, a condition shared with *Holonema westolli* (MILES, 1971, Fig. 6A). The snout is flat dorsally, but upturned, and its base is broad. The nostrils open ventrolaterally, and their dermal margin makes an open ring, closed laterally by a perichondral ossification (Fig. 6A).

On the ventral surface of the holotype, a dorsal, perichondral part of the right nasal capsule is preserved (n.cap; Fig. 6B). There is a posterior constriction, followed by a cylindrical canal, probably for the olfactory tract as in *Eastmanosteus calliaspis* (DENNIS-BRYAN, 1987, Fig. 16B).

Internasal plate (IN)

The limits of this plate are very clear on the radiograph of the holotype (Fig. 2). It appears as a broad, laterally extended plate. Its lateral margin is embayed, along the medial border of the incurrent nostril notch (nn), in a way which reminds of *Goodradigbeeon* (WHITE, 1978, Fig. 26D). The outer surface, or anterior lamina, is ornamented with large tubercles, which confirm its dermal origin (Fig. 6B). The recurrent lamina shows two symmetrical, shallow depressions which enclosed the ventral part of the nasal capsules, separated by a blunt, finely tuberculated, and basally enlarged internasal process (pr.in). The excurrent nostrils were probaly lying laterally to this process.

The internasal bone is known in *Coccosteus cuspidatus* (MILES & WESTOLL, 1968, Fig. 12 D-G), where it also contacts the rostral plate. Its dimensions are much smaller than in *Maideria*. According to GOUJET (1984: 215-216), the occurrence of an internasal plate in *Kujdanowiaspis* remains questionable.

Anterior superognathal (ASG)

This is the only known gnathal element. It is preserved in the holotype, and is still attached in its anatomical position to the endocranial ectethmoid process (Fig. 6B). It is a broad element,

FIG. 7. — *Maideria falipoui* n. g., n. sp. Holotype specimen, MCD 184. A, dorsal view. B, left lateral view. C, ventral view. Scale bar: 1 cm.

Maideria falipoui *n. g., n. sp. Holotype MCD 184. A, vue dorsale. B, vue latérale gauche. C, vue ventrale. Échelle : 1 cm.*

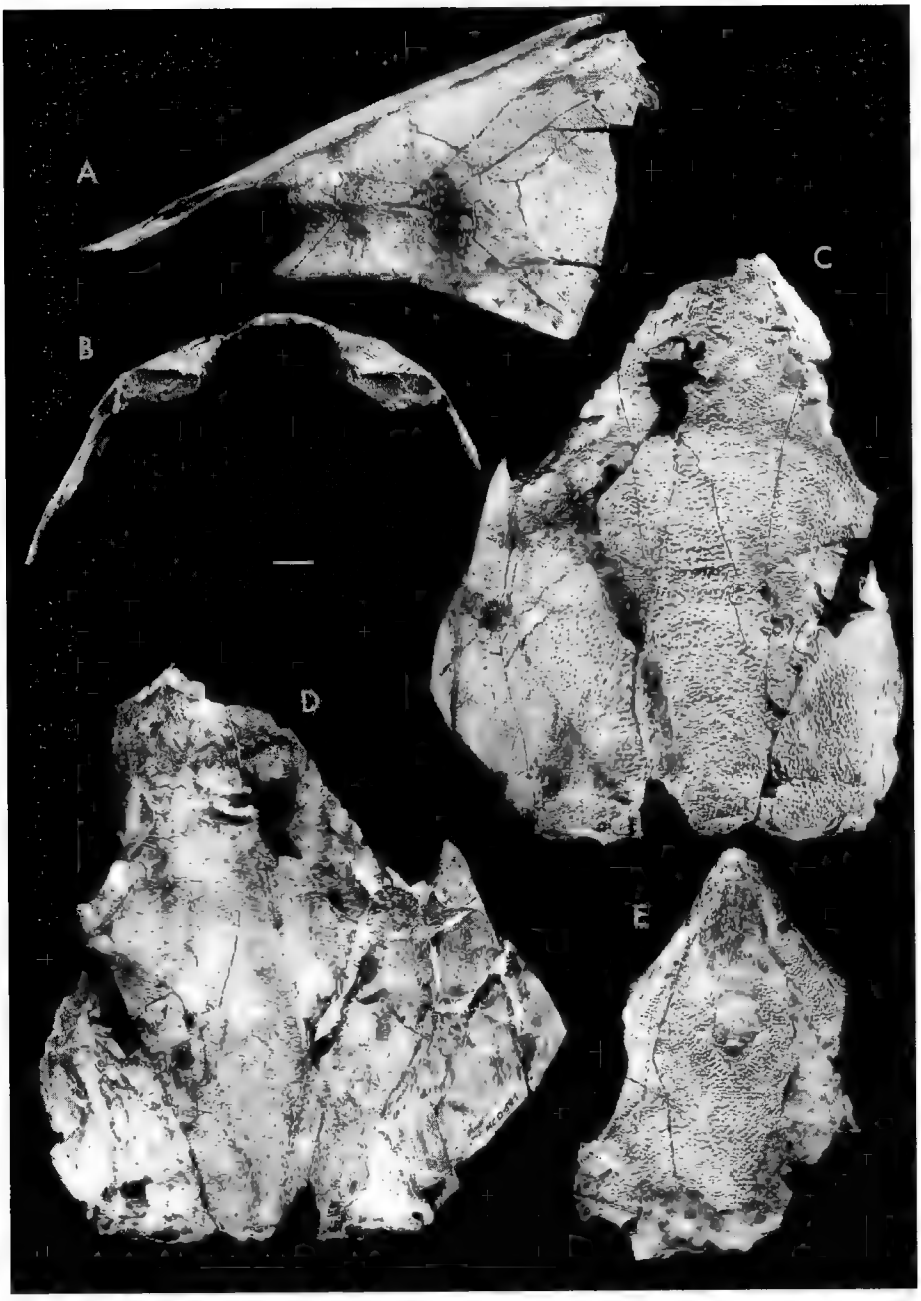


FIG. 8. — *Maideria falipoui* n. g., n. sp. A-D, specimen MCD 191. A, left lateral view. B, posterior view. C, dorsal view. D, ventral view. E, specimen MCD 197, dorsal view. Scale bar: 1 cm.

Maideria falipoui *n. g., n. sp. A-D, spécimen MCD 191. A, vue latérale gauche. B, vue postérieure. C, vue dorsale. D, vue ventrale. E, spécimen MCD 197 en vue dorsale. Échelle : 1 cm.*

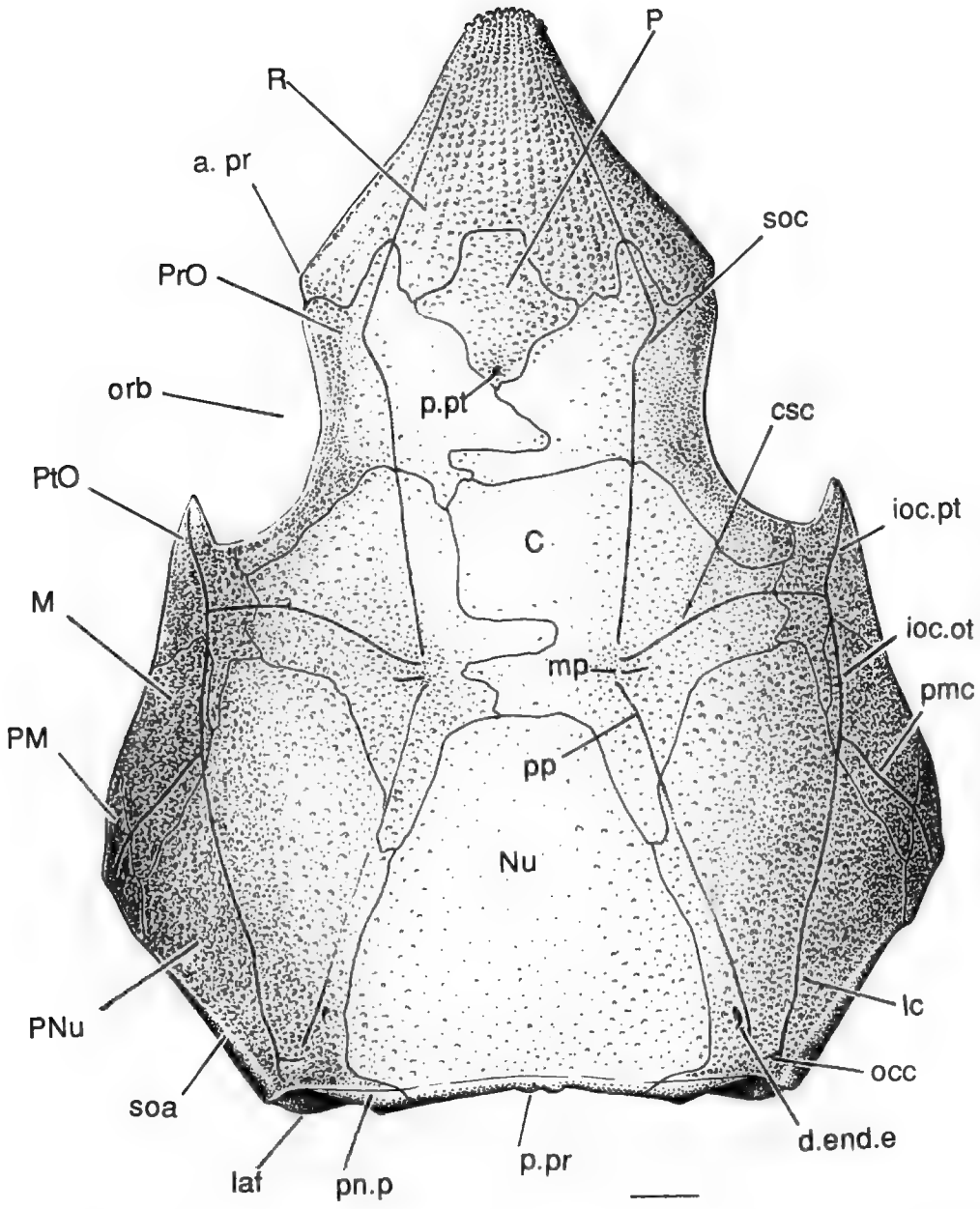


FIG. 9. — *Maideria falipoui* n. g., n. sp. Reconstruction of the skull-roof, dorsal view of MCD 184, 191, 197. Scale bar: 1 cm.

Maideria falipoui *n. g., n. sp. Reconstitution en vue dorsale du toit crânien. D'après les spécimens MCD 184, 191, 197. Échelle : 1 cm.*

the occlusal surface of which is depressed and covered with small pointed tubercles, which decrease in size from the periphery to the centre of the plate. Its anterior lateral and lateral margins bear a row of "teeth" (a.tr, l.tr; Fig. 6B). The plate projects medially as a narrowing process. Dorsally, the surface is gently curved transversally, but there is no dorsal process. This structure is considered to be one of the eubrachythoracid synapomorphy. The anterior superognathal of *Maideria* is plesiomorphic in lacking a dorsal process, and also in having an ornamented occlusal surface.

The gnathal element of primitive brachythoracids are poorly known in most of them, with only the posterior superognathal and the inferognathal described in *Goodradigbeeon* (WHITE, 1978, Figs. 24, 44-49), and the inferognathal known in *Antineosteus* and *Homostius*. Unfortunately, none of the gnathal elements is known in *Buchanosteus*. When compared with the dolichothoracid *Arctolepis* (GOUJET, 1984, Figs. 74, 82), the superognathal plate of *Maideria* shares the presence of a tuberculation on the occlusal surface. But it differs by its overall shape, rectangular, and lack of individualised teeth; no radial disposition of the "denticles" occurs.

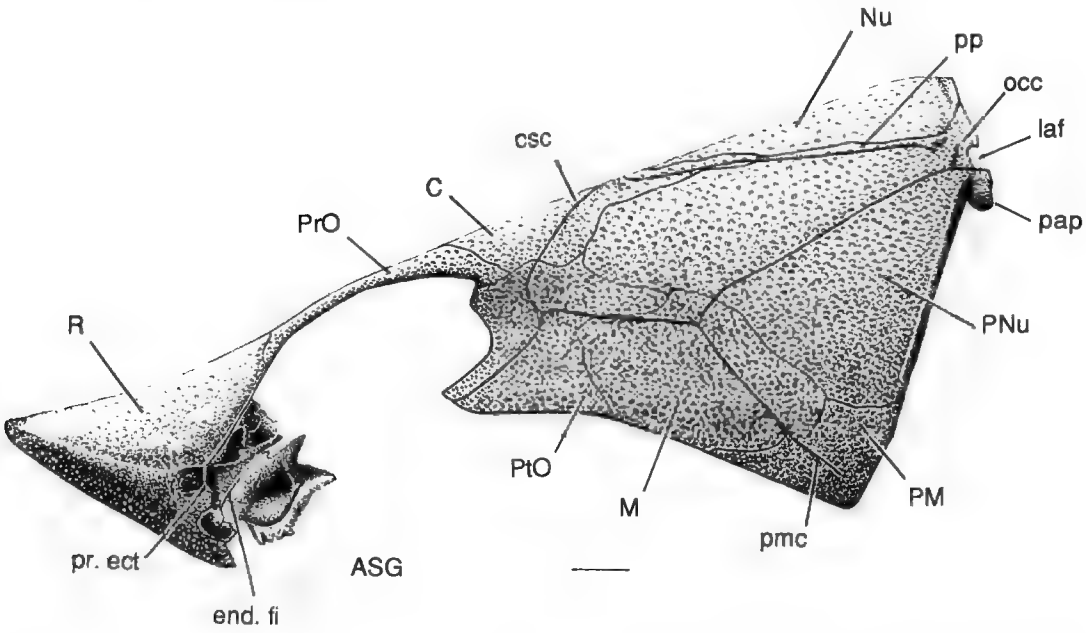


FIG. 10. — *Maideria falipoui* n. g., n. sp. Reconstruction of the skull-roof in left lateral view, based on MCD 184, 191, 197. Scale bar: 1 cm.

Maideria falipoui *n. g., n. sp. Reconstitution en vue latérale gauche du toit crânien. D'après les spécimens MCD 184, 191, 197. Échelle : 1 cm.*

Anterior ventrolateral plate (AVL)

The only specimen of this plate was associated with a portion of a typical rostral plate of *Maideria* (Fig. 11E-F) and is therefore referred to this genus. The anterior part is missing but

the posterolateral, posterior and medial margins are well preserved. The ornamentation consists of relatively small and scattered tubercles, which are larger in a lateral zone, near the ventral edge of the pectoral emargination (p. emb). The pectoral fenestra must have occupied a posterior position, much as in *Williamsaspis bedfordi* (WHITE, 1952, Figs. 1, 2), with which it also shares a long spinal margin. The surface of the bone at the level of the pectoral emargination is slightly bulging.

The posterior region of the visceral surface shows a contact surface for the posterior ventrolateral plate, with a ridge running forward from the posterior lateral corner to the centre of radiation of the plate.

The ventral thoracic shield of *Maideria* differs from that of *Antineosteus* and *Homostius* in having a posterior ventrolateral plate. The organisation of the thoracic shield may be closer to *Buchanosteus*, as figured by LONG (1984, Fig. 16F), where the spinal plate is large (WHITE & TOOMBS, 1972, Fig. 23) and the pectoral fenestra posteriorly closed.

Median dorsal plate (MD)

This plate (Fig. 11A-B) and a right anterior lateral plate are provisionally referred to *Maideria* on the only basis of the ornamentation, which is, however, a weak argument.

The median dorsal plate is longer than broad, with a straight anterior margin and a well-developed posterior process (pt.pr), not shown on figure 11A-B. The ornamentation is composed of small tubercles near the centre of radiation. At the periphery they tend to be arranged in lines, just as on the dorsal orbital margin and rostral plate of the skull-roof.

The ventral surface is concave, with two pairs of overlapping areas. The smaller anterior one is for the anterior dorsolateral plate (ADL cf.), and the posterior one for the posterior dorsolateral plate (PDL cf.). The ventral keel is barely developed anteriorly, but higher posteriorly and ends with a posteriorly excavated carinal process (cr.pr). These characters, and the general outline of the plate, evoke the median dorsal plate of *Buchanosteus* (WHITE, 1972, Fig. 17). An excavated carinal process occurs in eubrachythoracids, but is absent in other primitive brachythoracids when available.

Anterolateral plate (AL)

Only one complete plate of the right side is known (Figs. 11C-D, 12). It is broader than high, and its posterior margin is produced into a median process (pr.m). The postbranchial lamina is short and covered with pointed tooth-like denticles. The obstantic process (pr.ob) is anteriorly projected and hollowed by a small depression which represents the dorsal limit of the infraobstantic lamina (l.iob).

The inner surface shows a thin postbranchial crista (cr.pb.), the dorsal part of which bounds off a short contact area for the anterior dorsolateral plate (ADL cf.).

The posterior median process, the long ventral margin and the almost horizontal dorsal margin seem to be characteristic of *Maideria*, but an elongated anterior lateral plate is also found in camuropiscids (DENNIS & MILES, 1979b, Figs. 2, 12; LONG, 1988, Fig. 2; 1990, Fig. 1).

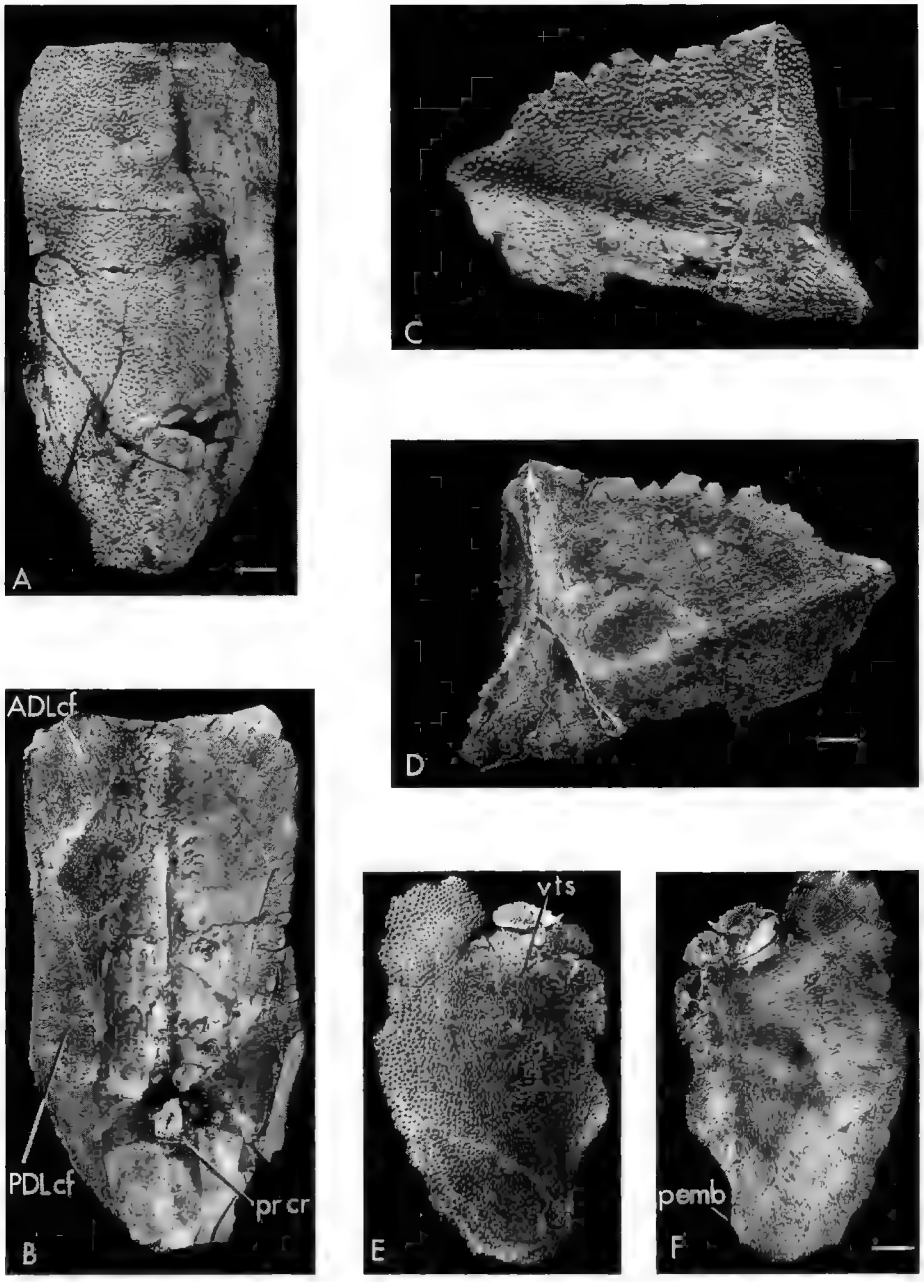


FIG. 11. — *Maideria falipoui* n. g., n. sp. A-B, specimen MCD 186, median dorsal plate. A, dorsal view, B, ventral view. C-D, specimen MCD 187, anterolateral plate. C, lateral view, D, medial view. E-F, specimen MCD 190, left anterior ventrolateral plate. E, ventral (outer) view; F, internal view. Scale bar: 1 cm.

Maideria falipoui *n. g., n. sp. A-B, plaque médiane dorsale, MCD 186. A, vue dorsale; B, vue ventrale. C-D, plaque latérale antérieure, MCD 187. C, vue latérale, D, vue interne. E-F, plaque ventrolatérale antérieure, MCD 190. E, vue externe, F, vue interne. Échelle : 1 cm.*

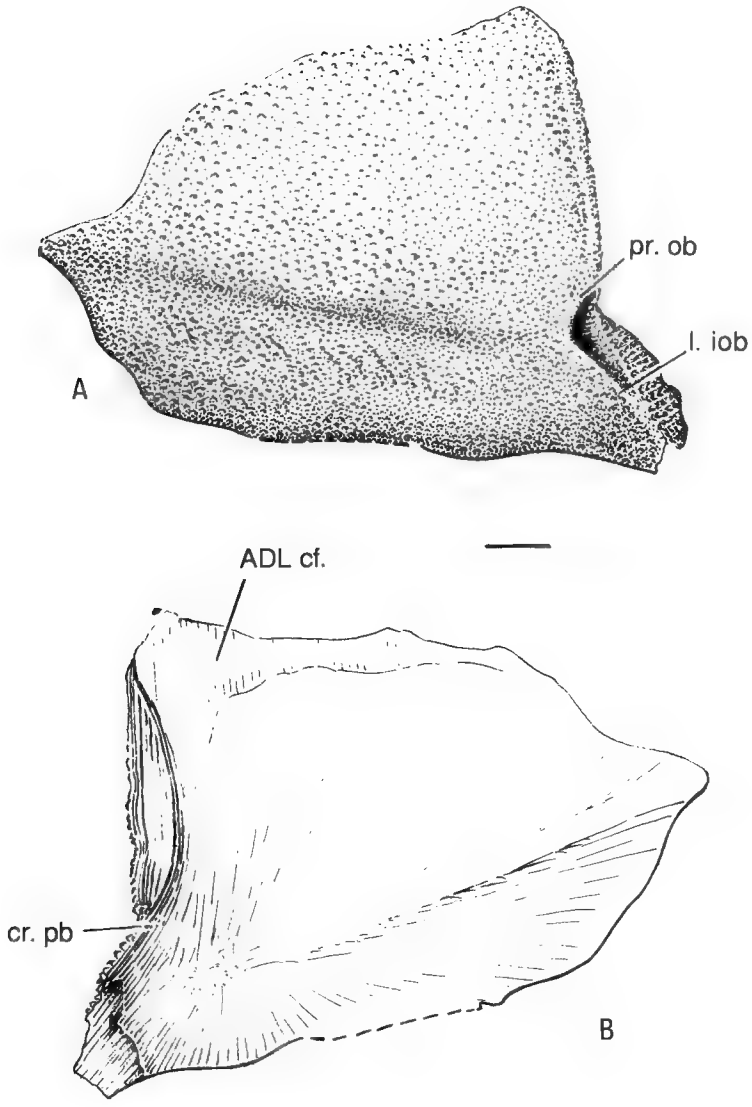


FIG. 12. — *Maideria falipoui* n. g., n. sp. Specimen MCD 187, anterior lateral plate. A, lateral view, B, medial view. Scale bar: 1 cm.

Maideria falipoui *n. g., n. sp. Plaque latérale antérieure, MCD 187. A, vue externe; B, vue interne. Échelle : 1 cm.*

PHYLOGENETIC ANALYSIS

Phylogenetic analyses of the "primitive brachythoracids" have been attempted by WHITE (1978), YOUNG (1979, 1981), LELIÈVRE (1984a, b; 1988), whilst the attention of the other workers has been drawn towards the interrelationships of eubrachythoracids (e.g. LONG, 1988; GARDINER & MILES, 1990; CARR, 1991). *Holonema* is always considered to be the most primitive brachythoracid; *Homostius* and *Buchanosteus* are good models for primitive brachythoracids. However the interrelationships of the 'primitive' brachythoracids are still unclear, probably because of the quite different patterns of the head and trunk shields. This situation is indirectly a consequence of the exceptional preservation and diversification of the Upper Devonian Gogo and Wildungen eubrachythoracid material, which has no equivalent for primitive brachythoracids. But some of the questions formulated by YOUNG (1981: 269) still have no answer.

A matrix of characters has been established in order to work out the interrelationships of the primitive brachythoracids; 53 characters have been defined from a matrix initially elaborated for brachythoracid interrelationships. This matter has been debated recently by CARR (1991), and will be discussed in connection with the description of Upper Devonian Moroccan brachythoracids.

CHARACTERS DEFINED ON THE SKULL-ROOF

1. Dermal plates of the skull-roof with overlapping surfaces: absent (0), present (1).

2. Structure of endocranial posterior postorbital process: two branches (0), one branch (1).

3. Development of a rostrum: absent (0), present and closed (1), present and tubular (2).

The derived pachyosteomorph *Oxyosteus* is not considered in this definition, its elongated rostrum is downturned and its anterior region remains unprepared on the original material.

4. Shape of rostral plate: broader than long (0), triangular in dorsal view (1), with a posterior process giving a 'T shape' outline (2), see CARR (1991).

5. Position of the anterior edge of the pineal plate, compared with the anterior edge of the orbit: posterior (0), anterior or on the same level (1).

6. Postnuchal process: absent (0), present (1).

7. Position of the levator muscle pits on the nuchal plate: posterodorsal (0), posteroventral (1), ventral (2).

8. Shape of the anterior nuchal margin on the dorsal surface: convex (0), straight (1), concave (2).

The primitive condition is indicated by dolichothoracids. CARR (1991: 372, character 10) retained a straight margin as the primitive state.

9. Shape of the posterior nuchal margin: straight (0), convex (1), concave (2).

10. Posterior nuchal thickening: present only under the paranuchal visceral surface (it corresponds to the development of the dermal articulation) (0), developed under all the occipital region of the skull-roof (1) (see LELIÈVRE *et al.*, 1990).

11. Length of nuchal and paranuchal plates: short (0), long (1).

The elongation of the nuchal and paranuchal plates could be associated with the elongation of the endolymphatic tube (see *Antineosteus*, LELIÈVRE 1984b, Fig. 3, Pl. 3C). Short paranuchal and nuchal plates do not seem to be correlated with a complete posterior consolidated arch, which is absent in *Maideria*. In the case of a complete development of this posterior arch, the endolymphatic tube remains short, and is sometimes included in the lateral part of the posterior thickening in certain Eubrachythoraci (e.g. *Dunkleosteus*). The position of the C/PNu/M or PtO triple point, relatively to the PNu/C/Nu triple point: posterior (0) or anterior (1), defined by CARR (1991, character 31) is probably correlated with this character and therefore is not used here.

12. Paranuchal plate process onto the central plate determining a lateral lobe: absent (0), present (1).

This character could also be identified when the anterior margin of the paranuchal is straight; this is the condition of *Maideria*. The position of the triple point PrO/PtO/C relative to the posterior triple point PtO/M/C or to PtO/PNu/C: parallels the midline or with the anterior point lateral (0), posterior point lateral to anterior point (1), as defined by CARR (1991, character 32), is another way to define the development of the lateral lobe of the central plates. The definition provided here is more simply expressed.

13. Shape of the condyle (or fossa) of the dermal articulation: ovoid (0), higher medially than laterally (1).

14. Suborbital plate: not overlapping the postorbital plate (0), overlapping the postorbital plate (1), (GARDINER & MILES, 1990, character 22.9; CARR, 1991, character 53).

15. Palatoquadrate as a single unit (0), separate quadrate and autopalatine ossifications (1), (MILES & DENNIS, 1979).

16. Preorbital plate embayment of the central plate: absent (0), present (1).

17. Posterior lobe of the central plate protrudring between the nuchal and paranuchal plates: absent (0), present (1).

18. Contact between central and marginal plates: present (0), absent (1).

The derived state occurred probably several times in placoderm history. VÉZINA (1990: 681) retained this character in his diagnosis of the plourdosteids. Although it is present in all the genera included in the Plourdosteidae (even *Torosteus*; GARDINER & MILES, 1990), it also occurs in other brachythoracids (e.g. *Maideria*, *Holonema*, *Pholidosteus*, *Tapinosteus*, *Enseosteus*, *Tafilalichthys*), and most of the actinolepid genera. It gives to this character a large distribution which could be interpreted as homoplastic. The long marginal plate of certain primitive brachythoracids obviously leads to a contact between the two plates, and could also be correlated with the development of the lateral lobe of the central plate.

19. Position of the contact between preorbital plates: posterior to the pineal plate (0), anterior (1), absence of contact (2).

The occurrence of a rostro-pineal plate does not influence the interpretation of this character, but in some dolichothoracids the condition is different. There is no contact in *Arctolepis*, and most actinolepids have a contact between the preorbital plates posterior to the pineal plate. Some phlyctaeniids show both conditions (e.g. *Heintzosteus*; GOUJET, 1984, Figs. 94, 97, 106). The pineal-preorbital region is usually broad in dolichothoracids and primitive brachythoracids. The relations and extent of these plates are probably determined by the presence of the rhino-ethmoidian fissure.

20. Dermal process on the preorbital plate: absent (0), present (1).

In eubrachythoracids the derived state may be correlated with the lateral position of the orbits (character 24). The dermal preorbital process is defined as the most anterior part of the dorsal orbital margin. The process could be developed from different plates in different groups: from the postnasal in *Dicksonosteus* and the camuropiscids but in a more ventral position, and from the rostropineal plate in *Buchanosteus*, in which the postnasal plate is still unknown. In eubrachythoracid, its occurrence implies a contact between the suborbital and preorbital plates, as the postnasal plates are more anteriorly placed and in contact with the anterior margin of the preorbital plate, the suborbital plate and the lateral margin of the rostral plate (see CARR, 1991: characters 17, 54; DENNIS & MILES, 1979b: 313, character 19). It is clear that a dermal preorbital process occurs when there is a contact with the suborbital plate, with the exception of *Homostius* and camuropiscids. In my opinion, *Homostius* and camuropiscids lack a preorbital dermal process; thus character 54 of CARR (1991) is correlated with the presence of the postnasal plate forming part of the orbit (CARR, 1991, character 26), or to the presence of a rostro-pineal plate, which is considered to be plesiomorphic for arthrodires. Finally the problem of the homology of the dermal preorbital process in these different groups will be resolved when more information will be available on *Buchanosteus*, and when the question of a possible fusion of the postnasal plates to the rostro-pineal plate will receive an answer. The plesiomorphic condition is a dermal preorbital process as part of the postnasal plate, a pattern shared by actinolepids (MARK-KURIK, 1973, Fig. 1A) and phlycateniids.

21. Posterolateral process of the postorbital plate: absent (0), present (1).

22. Composition of the dorsal orbital margin: preorbital and postorbital plates plus postnasal or rostral or rostropineal plates (0), preorbital and postorbital plates only (1).

The primitive state as defined here includes different plate arrangements in the dorsal orbital margin: the rostral plate in *Holonema*; the autapomorphic condition of *Antineosteus*, in which only the postorbital plate constitutes the dorsal orbital margin (coded as irrelevant in the data matrix); in *Buchanosteus*, the rostro-pineal plate forming the anterior corner of the orbit; the postnasal plate in *Dicksonosteus* and the camuropiscids; and finally the marginal plate in the posterior part of the orbital margin, in *Rhinosteus*, *Melanosteus* and other selenosteids.

23. Position and size of the orbits: small and anteriorly placed (0), small and laterally placed (1), enlarged and lateral (2).

This character seems to be correlated with the length of the contact between the cheek plates and the lateral margin of the skull-roof (CARR, 1991, character 61), and probably also to

the development of a suborbital lamina in eubrachythoracids (see LELIÈVRE, 1988, character 19). *Homostius* cannot be scored owing to its autapomorphic orbital position.

24. Triangular depression posterior to the supraorbital vault (CARR, 1991, character 3): absent (0), present (1).

In *Maideria*, the development of this depression is related to the presence of a well-defined dermal postorbital process. *Buchanosteus* is considered to show the derived state although the shape of the depression is elongated.

25. Length of the contact between cheek plates and the lateral margin of the skull-roof: long (0), short (1).

It is difficult to be precise as to the length of this contact. Here, the contact is rated on the basis of the comparison between the length of the lateral margin of the skull-roof and the width between the dermal articulations, which I consider as a stable proportion in brachythoracids (a short lateral skull-roof is less than twice this width).

26. Shape of submarginal plate: large (0), elongated (1), small and square (2).

The submarginal plate of primitive brachythoracids is known in *Buchanosteus* (YOUNG, 1979; WHITE & TOOMBS, 1972, Fig. 16), *Antineosteus* (LELIÈVRE, 1984b), *Homostius* (HEINTZ, 1934), and partly in *Goodradigbeeon* (WHITE, 1978). However the submarginal plate is identified without doubt only in *Antineosteus* and *Buchanosteus*. The relations with adjacent plates and the hyomandibular are difficult to determine for the other primitive brachythoracid genera. Two derived states have been distinguished, in contrast to CARR (1991, character 60) who coded only for one. Two derived states are necessary in order to take into account the condition in outgroup taxa and camuropiscids, because the anatomical relationships between the marginal and suborbital plates are unclear, and also whether or not they are in contact (CARR, 1991, character 55) is not an independent character. Those genera with a small, square-shaped and supposedly reduced submarginal (camuropiscids and *Rhinosteus*) have a contact between the marginal and the submarginal plates. Other character states, not included in this analysis, could be distinguished for advanced brachythoracids: submarginal plate elongated and vertical, or fused to the postmarginal plate, but they are not taken into account here.

27. Development of a suborbital lamina of the suborbital plate (LELIÈVRE, 1988: 293): absent (0), present (1).

This character seems to be correlated with the position of the orbit, although the disposition in *Homostius* is an exception. The derived state includes several bone patterns in different Late Devonian genera such as *Tafilalichthys* (LEHMAN, 1956), *Melanosteus* (LELIÈVRE *et al.*, 1987), *Gymnotrachelus*, and *Heintzichthys* (CARR, 1991). This problem, briefly discussed by LELIÈVRE *et al.* (1987), has been reviewed recently by CARR (1991).

CHARACTERS DEFINED ON THE GNATHAL PLATES

28. Dorsal process of the anterior superognathal: absent (0), present (1).

MILES (1971: 150, Fig. 59) described the anterior superognathal element of *Holonema westolli* as a small, unpaired, symmetrical plate. I agree with MILES' interpretation, and consider this gnathal element to lack a dorsal process strictly homologous to that of other brachythoracids.

29. "Teeth" developed on the occlusal surface of the anterior superognathal: absent (0), present on the anterior margin (1), present on anterior and lateral margins (2).

30. Occlusal surface of the anterior superognathal: denticulated (0), smooth (including crushing surface) (1).

The anterior superognathal of *Dicksonosteus* is unknown, but it can be assumed to be similar to the same denticulated element in *Arctolepis decipiens* (GOUJET, 1984, Fig. 82). It should be noted that the upper gnathal elements of the juvenile individuals of *Rolfosteus* are denticulated (DENNIS & MILES, 1979b: 306), but they are of a crushing type in the adults. Some Early Devonian actinolepids from North America have a denticulated inferognathal associated to an anterior crushing superognathal lacking denticles (D. GOUJET pers. comm.). Because of this ontogenetic and positional variation, the plesiomorphic state for arthrodires is questionable.

31. Inferognathal plate with a posterior non-biting portion: absent (0), present (1).

This character is used by MILES & DENNIS (1979), and CARR (1991). The non-biting blade portion of *Dunkleosteus* in HEINTZ's description (1932), may be linked with the presence of a single inferognathal ossification centre. It is not clear whether the occurrence of a ventral groove in the blade region is strictly homologous.

32. Occlusal surface of the inferognathal plate: denticles present (0), denticles absent (1).

The plesiomorphic state for this character is based on the morphology of this element observed in *Dicksonosteus* (GOUJET, 1984, Fig. 40), and on isolated actinolepid inferognathals (DENISON, 1958) referred to *Aethaspis* (D. GOUJET pers. comm.). Although the upper gnathal elements are broad and lack tubercles, the dorsal surface of the inferognathal is narrow, denticulated posteriorly, with two well-developed anterior denticles. There is no symphysial tooth, and the oblique anterior margin bears no denticle. The inferognathal of juvenile individuals of *Incisoscutum* exhibits the plesiomorphic character state (DENNIS & MILES, 1981, Fig. 12B-D).

33. Ventral surface of the inferognathal formed by a deep groove limited by two laminae, with the labial one more developed: presence of a deep groove and two laminae (0), absence of a groove (1).

In *Antineosteus* (LELIÈVRE, 1984b, Fig. 14B) and *Goodradigbeeon* (WHITE, 1978, Figs. 47-49), the ventral surface of the inferognathal is occupied by a deep groove. An isolated inferognathal from the Lower Devonian of Battery Point Formation (Québec), which probably belongs to the primitive brachythoracid *Forillonaspis* (PAGEAU, 1982), shows the same plesiomorphic condition. *Homostius* is coded as plesiomorphic according to MARK-KURIK (1992, Fig. 2).

REMARKS: The posterior superognathal element of *Goodradigbeeon* (WHITE, 1978, Figs. 44-46), and *Holonema westolli* (MILES, 1971) has a denticulated occlusal surface and is almost rectangular in shape, without a dorsal process. This suggests that in basal brachythoracids, in which the condition is unknown, the element should resemble dolichothoracids like *Dicksonosteus* (GOUJET, 1984, Fig. 82; Pl. 18.1) and *Actinolepis spinosa* (MARK-KURIK, 1985, Fig. 3).

WHITE (1952, Figs. 31-35) figured isolated posterognathal elements from the Early Devonian of the Goodradigbee River, which have a dorsal process and lack denticulation. They show the derived condition and belong to an eubrachythoracid.

REMARKS ON THE PARASPHENOID

The parasphenoid is known in the following brachythoracid genera: *Buchanosteus* (WHITE & TOOMBS, 1972, Figs. 5-7; YOUNG, 1979, Fig. 17; only the ventral surface is figured), *Antineosteus* (LELIÈVRE, 1988, Figs. 2A-C; 3A-C), *Coccosteus* (MILES & WESTOLL, 1968, Fig. 18A-B), *Panxiosteus* (WANG, 1979, Fig. 2), *Eastmanosteus calliaspis* (DENNIS-BRYAN, 1987, Fig. 17A-C), *Dunkleosteus* (DUNKLE & BUNGART, 1946), *Harrytoombsia* (MILES & DENNIS, 1979, Fig. 13A-D), *Pholidosteus* (STENSIÖ, 1963, Fig. 75), *Tapinosteus* (STENSIÖ, 1963, Fig. 63A-B), *Incisoscutum* (DENNIS & MILES, 1981, Figs. 13, 15), *Tafilalichthys* (LELIÈVRE, 1991, Fig. 4), *Bullerichthys*, *Bruntonichthys* (DENNIS & MILES, 1980, Figs. 3C-D; 9A-C), *Melanosteus* (LELIÈVRE *et al.*, 1987, Pl. 2C-E), *Trematosteus* (STENSIÖ, 1963, Figs. 87A, 92A), *Brachyosteus* (STENSIÖ, 1963: 352, but still not figured), *Erromenosteus* (STENSIÖ, 1963, Fig. 115E-G), *Pachyosteus* (STENSIÖ, 1963, Fig. 115H-J), *Torosteus* (MILES & GARDINER, 1990, Figs. 9, 24), *Latocamurus* (LONG, 1988, Fig. 11), *Heintzichthys* (CARR, 1991, Fig. 8A-C) and *Titanichthys* sp. (pers. observ. in the Cleveland Museum collections).

Buchanosteus and *Antineosteus* are considered as primitive brachythoracids and their parasphenoids share some characteristics. In both genera, the parasphenoid is short and broad without a developed prehypophysial region, the ventral surface is tuberculated. Because of the poor information on the parasphenoid of other primitive brachythoracid genera, they have not been used herein. Nevertheless, it seems that there is a tendency towards an elongation of the prehypophysial region, the disappearance of the palatine tuberculation, the development of a median crista on the ventral surface, and the disposition of the groove for the carotid artery (K. DENNIS-BRYAN, pers. comm.; CARR, 1991).

CHARACTERS DEFINED ON THE THORACIC ARMOUR

34. Posterior margin of the pectoral fenestra: closed (0), open (1).

Primitive brachythoracids display both closed and open pectoral fenestrae. The latter condition is seen in *Antineosteus* and *Homostius* which lack the posterior ventrolateral and posterior median ventral plates. Probably the posterior opening of the pectoral fenestra occurred at least twice in brachythoracid evolution in different ways. The opening of the fenestra occurs either by a loss of the posterior plates (see character 36), or by the loss of contact between the posterior lateral and posterior ventrolateral plates (pachyosteomorph arthrodires), or by a combination of both. Some brachythoracids have lost the posterior lateral plate (e.g. *Holonema* and *Incisoscutum*; GARDINER & MILES, 1990: 198).

35. Length of the lateral pectoral process of the spinal plate: long (0), short (1).

Primitively the spinal plate was in contact with three plates: (e.g. *Dicksonosteus* and *Arctolepis*), the anterior lateral plate dorsally, the interolateral plate anteriorly and the anterior ventrolateral plate ventrally. Thus a separation between the anterior lateral and anterior ventrolateral

plates is considered to be the plesiomorphic condition. *Homostius* shows this condition because of a short spinal plate (pseudospinal of DENNIS & MILES, 1981) and a pectoral incision (MARK-KURIK, 1963). Four genera analysed in this study lack information concerning the spinal pattern with adjacent plates: *Antineosteus*, *Taemasosteus*, *Arenipiscis*, *Maideria*. With the exception of camuropiscids, the remaining genera have a spinal contact with the three adjacent plates mentioned above. Camuropiscids lack a contact between the spinal and the interolateral plates because the spinal is limited to a posterior position giving an anterior contact between the anterior lateral and ventrolateral plates. Thus two characters used by CARR (1991), [interolateral-spinal contact (his character 38) and anterior lateral–anterior ventrolateral plates contact (his character 40)] define the same anatomical dispositon. When there is a contact between the anterior lateral plate and the anterior ventrolateral plate, then there is no contact between the interolateral plate and the spinal plate, a pattern which is exclusive to camuropiscids.

Only the interolateral and spinal plates contact has been scored. The plesiomorphic state [(0) = present] is defined referring to the conditions of *Dicksonosteus* (GOUJET, 1984: 137, Fig. 72C) and *Arctolepis decipiens* (GOUJET, 1984, Figs. 86, 87). This character polarity differs from that of CARR (1991), whose coding statement may be wrong, based on the *Dicksonosteus* pattern (see CARR, 1991, characters 38-40). This contact is long in camuropiscids, because the spinal plate has a posterior position [see DENNIS & MILES (1979b: 325), CARR (1991: 374, character 38)].

36. Posterior ventrolateral and posterior median ventral plates: present (0), absent (1).

The absence of these plates could be concluded from the straight posterior margin of the anterior ventrolateral plate and/or from the absence of a contact surface on its visceral surface. This character is correlated with an open pectoral fenestra (character 34), but is treated separately because we have no precise idea of the process implied in the opening of the pectoral fenestra in each genus. This character is not treated as two separate characters, because no taxon shows the loss of one of the two plates.

37. Orientation of the postbranchial lamina of the interolateral plate and of the anterior border of the anterior lateral plate. Straight, in dorsal view, with a lateral branchial space anteriorly inclined (0), convex in dorsal view, with a lateral branchial space either slightly inclined anteriorly or nearly vertical (1).

The anterior border of the anterior lateral plate defines the orientation of the branchial space.

38. Shape of the median dorsal plate: longer than broad (with or without a posterior spine) (0), shorter than broad (1).

39. Median dorsal plate with a posterior expansion or spine: present (0), absent (1).

The plesiomorphic character state is coded by CARR (1991) as a rounded posterior region (no posterior expansion). I consider the condition in *Dicksonosteus* to be plesiomorphic, that is, a posteriorly rounded posterior expansion. A similar condition is present in others dolichothoracids such as *Heintzosteus* (GOUJET, 1984, Fig. 106 B), and *Arctolepis decipiens* (GOUJET, 1984, Figs. 86, 87) which have a pointed posterior pointed.

40. Ventral surface of median dorsal plate: presence of a longitudinal groove (0), presence of a keel and a carinal process (1), presence of a posteriorly excavated carinal process (2).

GARDINER & MILES (1990: 192) did not distinguish the second derived state of this character, which is constant at the eubrachythoracid level. However a posteriorly excavated carinal process is not always correlated with the occurrence of a posterior expansion, because *Dunkleosteus* has a short median dorsal plate with a posteriorly excavated carinal process.

41. Branchial lamina of the interolateral plate: unornamented with a short ventral lamina (0), ornamented with a short ventral lamina (1), ornamented with a large ventral lamina (2).

The plesiomorphic state for this character is based on the interolateral plate of *Dicksonosteus arcticus* (GOUJET, 1984, Fig. 65), but the same character state is also found in some pachyosteomorph arthrodires [e.g. *Tafilalichthys lavocati* and *Heintzichthys gouldii* (CARR, 1991, Fig. 9B, C)] in which it could be parallely derived.

42. Anterior lateral plate with a high dorsal lamina (YOUNG, 1981): absent (0), present (1).

No characteristic can be defined on the scapulocoracoid as it is only known in *Buchanosteus* (WHITE & TOOMBS, 1972, Fig. 18; Pl. 9, Fig. 4). In this genus, the scapulocoracoid is short with a closed pectoral fenestra, but we ignore what is its length in primitive brachythoracids with an open pectoral fenestra (e.g. *Antineosteus*, *Homostius*), although the development of the spinal plate and its relationship with the scapulocoracoid may be involved. The scapulocoracoid is known but incomplete in *Holonema westolli* (MILES, 1971, Fig. 91).

CHARACTERS USING SENSORY LINES

43. Supraorbital sensory line on the rostral plate: absent (0), present (1).

44. Supraorbital sensory line on the central plate (YOUNG, 1981): absent (0), present (1).

45. Position of the otic branch of the infraorbital sensory line on the marginal plate: near the lateral margin of the plate (0), near the medial margin of the plate (1).

46. Postsuborbital sensory line on the suborbital plate: absent (0), present (1) (primitive brachythoracid synapomorphy *in* LELIÈVRE, 1988: 294).

47. Relation between the supraoral and infraorbital sensory lines on the suborbital plate: connected (0), separate(1).

The supraoral sensory line may be absent on the suborbital of certain pachyosteomorphs (e.g. *Tafilalichthys*) and certain genera from the Upper Devonian Cleveland Shales and is not scored here.

48. Orientation of the occipital cross-commissure: directed towards or reaching the nuchal plate (0), directed onto the nuchal gap, and extending on the extrascapular plates, if preserved (1), absent (2).

The primitive state has been defined after the condition met within *Arctolepis decipiens*, with an occipital commissure crossing the nuchal plate (GOUJET, 1984, Fig. 77, see also *Buchanosteus*, YOUNG, 1979, Fig. 1).

49. Ventral sensory line on the anterior ventrolateral plate: absent (0), present (1). See CARR (1991, character 79) and MILES (1971, Fig. 108).

50. Main lateral sensory line on the posterior dorsolateral plate: absent (0), present (1).

51. Main sensory line as a groove on the median dorsal plate: absent (0), present (1).

52. Suborbital sensory pits: absent (0), present (1).

53. Angle between the suborbital and postorbital branches of the infraorbital sensory line: open (more than 90°) (0), closed (less than 90°) (1).

PHYLOGENETIC PATTERNS

Only seven genera of "primitive brachythoracids" have been taken into account in this analysis. Others 17 primitive brachythoracids taxa have been described in the literature, but most of them are too poorly known to be coded in the matrix. Those taxa are:

Jiushengshia longoccipita Wang & Wang, 1983
Euleptaspis depressa Gross, 1933 and the *Euleptaspis* species A and B mentioned by ØRVIG (1969)
Errolosteus goodradigbeensis Young, 1981
Goodradigbeeon australianum White, 1978
Kueichowlepis sinensi P'an, Wang & Liu, 1975
Burrinjucosteus asymmetricus White, 1978
Williamsaspis bedfordi White, 1978
Gemuendenaspis angusta Miles, 1962
Forillonaspis lehmani Pageau, 1982.

These genera share some characters either with the Migmatocephala or with brachythoracids as defined here (Migmatocephala plus Eubrachythoraci). The different species of *Homostius* are not discussed, and only *Homostius sulcatus* is scored in the matrix, based on HEINTZ's description (1934), completed by MARK-KURIK (1992: 177-178). *Holonema* has been coded by using the complete description of *Holonema westolli* by MILES (1971), from the Frasnian of Gogo. *Tityosteus rieversi* has been coded on the basis of OTTO's description (1992).

Two outgroups have been coded – *Dicksonosteus* and *Arctolepis* – they were chosen mainly because of their completeness. Fifty three characters have been defined of which fourteen are multistate characters, 51% of the characters are defined on the skull-roof, 11.3% on the gnathal elements, 17% on the thoracic armour and 20.7% on the sensory lines pattern. An analysis of the 53 unweighted and unordered characters (Deltran optimization) and Branch and Bound algorithm with PAUP (SWOFFORD, 1991) gave 17 equally parsimonious topologies (CI = 0.583, HI = 0.443) with 115 evolutionary steps. In those topologies the position of *Arenipiscis* was the most ambiguous.

Arenispiscis westolli (YOUNG, 1981) is the most incomplete taxon included in this set of brachythoracids, 47.1% of its characters are coded. Its deletion is an important gain because

only 4 topologies at 110 evolutionary steps are found, with the following indices: CI = 0.600, HI = 0.427, RI = 0.654, and its deletion may be argued for only on the basis of the largest number of missing data (see CLOUTIER, 1991: 410). Most of the other taxa were fairly complete with regard to the characters studied: *Dicksonosteus* (94.3% of all characters), *Arctolepis* (96%), *Antineosteus* (86.8%), *Homostius* (86.8%), *Buchanosteus* (83%), *Holonema westolli* (98.1%), *Taemasosteus* (60.3%), camuropiscids, *Coccosteus cuspidatus*, *Incisoscutum ritchei* (100%), *Maideria* (73.5%), *Tityosteus* (54.7%). Nevertheless, *Arenipiscis* shares with the Migmatocephala their two synapomorphies 11 [1] and 38 [1].

In these four equally parsimonious topologies a reversal on character 26 [1 → 0] for one of the topologies at the node uniting *Holonema* to the clade A and clade B is considered as impossible. In fact this reversal implies the transformation of an elongated submarginal plate – the condition met with in *Coccosteus cuspidatus* – to the condition met in *Holonema*, which has a very large plate. The morphological structure retained in the definition of that character concerns the overall shape of the submarginal plate, but it appears to be unprecised, as it concerns only the shape of this plate and not, for example, the overlapping surfaces and the relationships of the submarginal plate with the adjacent plates, which could be potentially more informative. But the submarginal is rarely preserved and the definition and the coding of the overlapping surfaces is difficult to establish for each taxon considered here. So this character has been deleted. The run of PAUP in this new condition gave three equally parsimonious topologies at 108 evolutionary steps, with a CI = 0.602, HI = 0.426, RI = 0.656 (see Fig. 13 A-C).

A run of PAUP with character 26 ordered gives four equally parsimonious trees with 111 evolutionary steps. Three of the four topologies are the same as the one discussed (Fig. 13A-C). In the fourth topology *Holonema* is placed as the sister taxon of the Migmatocephala and Eubrachythoraci; in this case character 26 [1] is a uniquely shared derived character for the basal brachythoracid clade, along with an inferognathal plate with a non-biting posterior portion, that is, character 31 [1]. This topology expresses the current opinion of authors about the phylogenetic position of *Holonema* within the brachythoracids. This position of *Holonema* rests on the congruence of both characters, as a run of PAUP with the deletion of character 31 gives three equally parsimonious topologies in which *Holonema* is placed in the Eubrachythoraci (as in Fig. 13A-C). In the analysis provided here I shall retain the run with all characters unordered.

In the strict consensus tree (Fig. 14; Mikevitch CI = 0.520), three major monophyletic groups are identified. The basal brachythoracid clade, and two basal clades, the Migmatocephala, or clade A, and the eubrachythoracid, or clade B, respectively.

For a long time the monophyly of brachythoracids has been recognized and diagnosed by different authors (YOUNG, 1979; GOUJET, 1984; CARR, 1991). At this node four synapomorphies given by those authors, are retained of which three are unique shared derive features:

— dermal plates of the skull-roof developping overlapping surface 1 [1];
— one branch in the posterior endocranial postorbital process 2 [1];
— presence of a postnuchal process 6 [1].

Character 35 [1] (short lateral pectoral process of the spinal plate) is retained as a synapomorphy for brachythoracids only when *Buchanosteus* and *Maideria* are respectively the sister taxa of clade A and clade B (Fig. 13B).

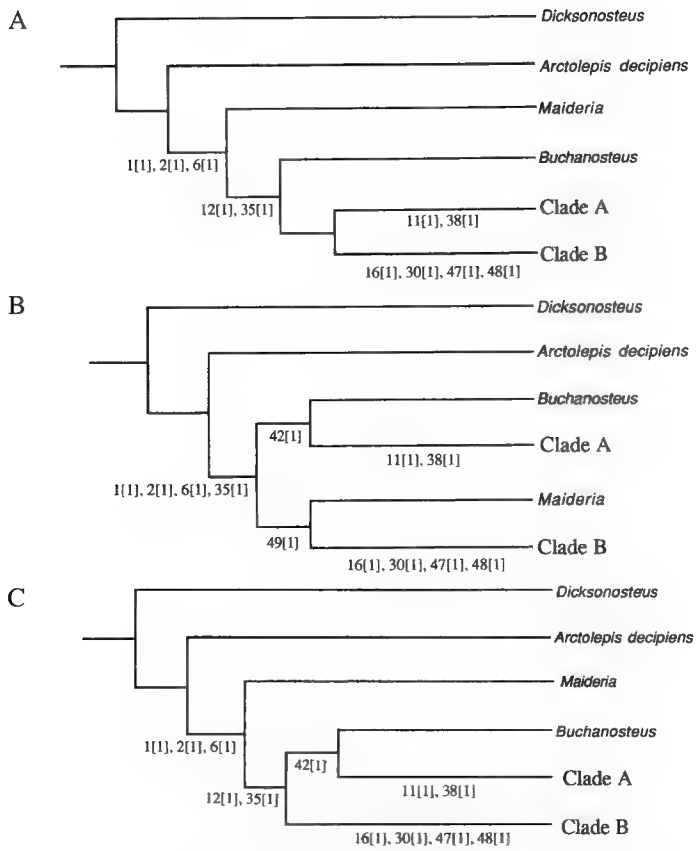


FIG.13. — A-C, three equally parsimonious topologies of the interrelationships among brachythoracids. From a matrice of 53 unordered characters, 107 steps, from with PAUP 3.0S. The statistics are: CI = 0.602, HI = 0.430, RI = 0.656. The synapomorphies occuring at each nodes are placed in brackets. Clade A for the Migmatocephala, clade B for the Eubrachythoraci.

A-C, trois topologies également parcimonieuses des relations de parenté des Brachythoracii à partir d'une matrice de 53 caractères non ordonnés par PAUP (CI = 0,602; HI = 0,430 ; RI = 0,656) (version 3.0s). Les synapomorphies retenues à chaque nœud sont indiquées entre crochets. Les Migmatocephala correspondent au clade A et les Eubrachythoracii correspondent au clade B.

The basal brachythoracid clade is diagnosed also by six homoplastic characters of which four are shared in each one of the three topologies (Fig. 13A-C):

— presence of a posterior lobe of the central plate which protrudes between the nuchal and the paranuchal plates 17 [1 (CI = 0.500)];

— median dorsal plate with a carinal process posteriorly excavated 40 [2] (CI = 0.667);

— presence of the supraorbital sensory line on the central plate 44 [1] (CI = 0.667);

— presence of the otic branch of the infraorbital sensory line near the medial margin of the marginal plate 45 [1] (CI = 0.500).

Two homoplastic characters, 21 and 46, appear in the topologies 1, 2 and 3 respectively (Fig. 13A-C). Character 21 [1] presence of a posterolateral process of the postorbital plate. In the topology 1 (Fig. 13A), this character has a low value CI = 0.333, and supports a reversal at the basal cubrachythoracid clade (clade B), because camuropiscids and *Incisoscutum* share the plesiomorphic state of that character, and *Coccosteus cuspidatus* shares the apomorphic state with both clade A, *Buchanosteus* and *Maideria*. In the two other topologies, character 21 does not support a reversal because of the respective position of *Buchanosteus* and *Maideria* (Fig. 13B-C). Character 46 [1] presence of a postsuborbital sensory line on the suborbital plate. This character (CI = 0.500) supports a reversal ($1 \rightarrow 0$) in the basal clade [*Coccosteus cuspidatus* + *Incisoscutum*] as camuropiscids share the plesiomorphic state with clade A (*i.e.* a postsuborbital sensory line on the suborbital plate).

Two other basal clades are defined in the strict consensus tree, the Migmatocephala (WHITE, 1972) referred to as clade A, and the Eubrachythoraci, or clade B.

THE BASAL CLADE MIGMATOCEPHALA

This clade is diagnosed by two uniquely shared derived character (CI = 1.000):

— long nuchal and paranuchal plates 11 [1] and;

— median dorsal plate shorter than broad 38 [1].

Three homoplastic characters (39, 40 and 42) occur at this node of which only one is common to all topologies (Fig. 13A-C):

— the absence of a posteriorly excavated carinal process (see above for the homoplastic characters of the basal brachythoracid clade) 40 [1] (CI = 0.667). The explanation for this transformation [$2 \rightarrow 1$] is the occurrence of the apomorhic state in *Maideria*; and the presence of the plesiomorphic state in *Holonema*, which led to consider this genus as a "primitive" brachythoracid (YOUNG, 1981, Fig. 5).

The two other homoplastic characters are:

— absence of a posterior spine of the median dorsal plate 39 [1] (CI = 0.333). This homoplasy occurs in the topology 2 and 3. It supports a reversal in *Coccosteus cuspidatus* in the three topologies (presence of the plesiomorphic state), and appears in parallel in the basal clade B in the topologies 2 and 3 (Fig. 13B-C), its CI (CI = 0.333) has a low value;

— presence of a high dorsal lamina of the anterior lateral plate 42 [1] (CI = 0.500) in the topology 1 when *Buchanosteus* is the sister taxon of [clade A + clade B]. On the contrary this character is interpreted as a uniquely shared derived character in the topologies 2 and 3 (Fig. 14B-C), when *Buchanosteus* is the sister taxon of clade A.

Two clades are diagnosed in clade A. The first one is the clade [*Tityosteus* + [*Antineosteus* + *Homostius*]] and is supported by one synapomorphy;

— absence of the occipital cross-commissure 48 [2]. And two homoplastic characters;

— a medially higher articular condyle of the anterior dorsolateral plate 13 [1] (CI = 0.333), a character which is parallely derived in *Holonema*;

— a pectoral fenestra open by absence of the posterior ventrolateral plate 34 [1] (CI = 0.500).

Character 13 [1] is derived parallely in *Holonema* and *Buchanosteus* in the three topologies, like character 34 [1] which appears in parallel in *Incisoscutum*, even though this genus still has posteroventral and posteromedian ventral plates.

The other clade [*Antineosteus* + *Homostius*] is supported by a single uniquely derived character:

— absence of posterior lateral and posterior ventrolateral plates 36 [1].

Four homoplastic characters are common in the three topologies:

— posteroventral position of the levator muscles pits on the ventral surface of the nuchal plate 7 [1] (0.667);

— no overlapping contact between the suborbital and postorbital plates 14 [1] (CI = 0.333). This character supports two reversals in the topology 1, of which one occurs in *Holonema*, and one reversal in the topologies 2 and 3. The latter reversal is common to all topologies;

— inferognathal with a posterior non biting portion 31 [1] (CI = 0.500). This character is parallely derived in clades [*Antineosteus* + *Homostius*] and [camuropiscids + [*Coccosteus cuspidatus* + *Incisoscutum*]];

— no supraorbital sensory line on the central plate, 44 [1 → 0] (CI = 0.667). This character, coded as polymorphic in *Arctolepis decipiens*, supports a reversal at this node in each topology.

THE BASAL CLADE EUBRACHYTHORACI

The basal Eubrachythoraci clade, or clade B, is supported by four uniquely shared derived characters (CI = 1.000):

— preorbital plate embayment of the central plate 16 [1];

— no denticulation on the occlusal surface of the anterior superognathal plate 30 [1];

— supraoral and infraorbital sensory lines connected on the suborbital plate 47 [1] and;

— occipital cross-commissure directed toward the nuchal gap and/or present on the extrascapular plates 48 [1].

Nine homoplastic characters support this clade, of which only three are common to the three topologies (Fig. 13A-C), they are:

— a posterior position of the anterior edge of the pineal plate compared to the anterior edge of orbit 5 [1 → 0] (CI = 0.500). This character supports the same reversal in *Tityosteus*;

— small and laterally placed orbits 23 [1] (CI = 0.750);

— an ornamented branchial lamina with a large ventral lamina of the interolateral plate 41 [2] (CI = 0.667). This character supports a reversal in *Coccosteus cuspidatus* as a terminal taxon which has a short ventral lamina of interolateral plate (41 [1]).

The other six homoplastic characters supporting this clade B are:

— paranuchal plate process onto the central plate determining a lateral lobe 12 [1] (CI = 0.500). This homoplasy is parallely derived for the clade A;

— no contact between central and marginal plates 18 [1] (CI = 0.333). This homoplasy is common to the topologies 1 and 3 for the clade Eubrachythoraci;

— loss of contact between preorbital and pineal plates 19 [2] (CI = 0.400). This character supports a reversal for camuropiscids (19 [1 → 0]), and is parallely derived in *Homostius* and *Tityosteus* in both topologies 2 and 3;

— absence of posterolateral process of the postorbital plate 21 [1 → 0] (CI = 0.333). This character is a reversal in the topology 1 (see discussion on this character in the diagnosis of basal clade A);

— median dorsal plate without a posterior spine 39 [1] (CI = 0.333). This character is homoplastic with respect to the clade Migmatocephala and supports a reversal [1 → 0], in *Coccosteus cuspidatus* as a terminal taxon in both topologies 2 and 3;

— presence of a ventral sensory line on the anterior ventrolateral plate 49 [1] (CI = 0.500). This character is parallely derived in *Maideria* as a terminal taxon, in topologies 1 and 3, and constitutes a uniquely shared derive character in topology 2, for the clade uniting *Maideria* and clade B as sister taxa.

Within the basal clade Eubrachythoraci a monophyletic group units [camuropiscids + [*Coccosteus cuspidatus* + *Incisoscutum*]] and is diagnosed by six uniquely shared derived characters in each one of the three topologies (Fig. 13A-C):

— a concave posterior margin of the nuchal plate, 9 [1];

— a continuous posterior nuchal thickening under the entire occipital region of the skull-roof, 10 [1];

— separate quadrate and autopalatine ossifications, 15 [1];

— the presence of a dorsal process of the anterior superognathal, 28 [1];

— an occlusal surface of the inferognathal plate without denticle, 32 [1];

— the interolateral postbranchial lamina, and the anterior border of the anterolateral plate convex in dorsal view with a lateral branchial space anteriorly inclined, 37 [1].

Seven homoplastic characters are retained at this level, of which five are common to each topology:

— triangular shape of the rostral plate in dorsal view, 4 [1] (CI = 0.500);

— a short contact between the cheek plate and the lateral margin of the skull-roof 25 [1] (CI = 0.500). Character 25 is homoplastic (parallely derived) with respect to *Maideria*;

— development of "teeth" on anterior and lateral margins of the occlusal surface of the anterior superognathal plate, 29 [2] (CI = 0.667). This character supports the transformation (29 [2 → 1]) for camuropiscids in each topology;

— inferognathal plate with a posterior, non-biting portion 31 [1] (CI = 0.500). Character 31 is also homoplastic (parallely derived) with the clade [*Antineosteus* + *Homostius*] in the three most parsimonious topologies (Fig. 13A-C);

— absence of a deep groove limited by two lamina on the ventral face of the inferognathal, 33 [1] (CI = 0.500). This character is parallely derived in *Homostius*.

Two more homoplastic characters appear independently in topology 2 and 3:

— the posteroventral position of the fossa for the levator muscles on the ventral face of the nuchal plate, 7 [1]. This multistate homoplastic character is retained also at the node uniting the basal clade A and *Buchanosteus* in topology 2;

— suborbital plate overlapping postorbital plate, 14 [1] (CI = 0.333). This character supports a reversal (14 [1 → 0]), at the basal node of the clade [*Antineosteus* + *Homostius*] in topologies 2 and 3.

The three most parsimonious topologies differ by the position of two taxa, *Buchanosteus* and *Maideria*. In topology 1 (Fig. 13A), *Buchanosteus* is excluded from clade A because it does not share synapomorphies 11 [1] and 38 [1], and *Maideria* from clade B because it does not share synapomorphies 16 [1], 30 [1], 47 [1], 48 [1] which diagnose it. The characters 12 [1] and 35 [1] are synampomorphies supporting the clade [*Buchanosteus* + [clade A + clade B]].

In topology 2 (Fig. 13B), the node uniting *Buchanosteus* and clade A is diagnosed by synapomorphy 42 [1] (an anterior lateral plate with a high dorsal lamina), and by eight homoplastic characters (7 [1], 8 [2], 12 [1], 14 [1], 21 [1], 26 [1], 41 [1], 51 [1]). *Maideria* is united to clade B by sharing synapomorphy 49 [1] (presence of a ventral sensory line on the anterior ventrolateral plate), and one homoplasy (character 18 [1]).

In topology 3 (Fig. 13C), *Buchanosteus* is linked to clade B by the same synapomorphy as in topology 2, and also by six homoplasies (8 [2], 14 [1], 21 [1], 26 [1], 41 [1], 52 [1]), which are common to topology 2. In topology 3, the node uniting [clade B + [*Buchanosteus* + clade A]] is supported by two homoplastic characters (46 [1] and 7 [1]) and by two uniquely shared derive characters: paranuchal plate process determining a lateral lobe of the central plate (12 [1]), and by a short lateral pectoral process of the spinal plate (35 [1]).

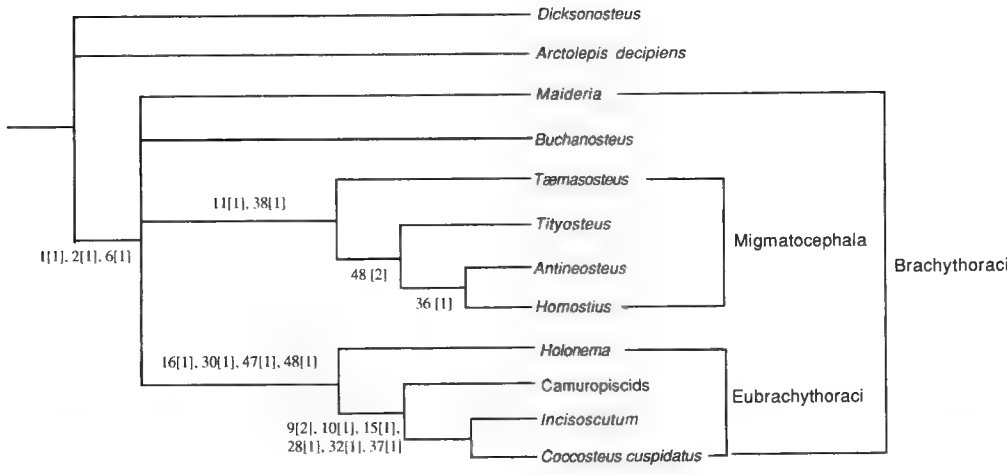


FIG. 14. — Strict consensus tree of the three topologies, with a classification of brachythoracids, from PAUP 3.0 s, at 107 steps including 12 taxa and 53 unordered characters. The synapomorphies occuring at each nodes are placed in brackets.

Arbre consensus strict des trois topologies également parcimonieuses, avec une classification des brachythoracides obtenue à partir de PAUP 3,0 s (108 pas, 12 taxa, 53 caractères non ordonnés). Les synapomorphies définissant chaque nœud sont placées entre crochets.

SYSTEMATIC REMARKS

Compared with the phylogenetic analysis of CARR (1991, Fig. 20) the phylogenetic scheme presented herein (Fig. 14) is more resolved with respect to relationships of the whole brachythoracids, except for pachyosteomorph relationships which are not the topic of this analysis. The definition of the monophyly of the "primitive brachythoracids" given by CARR (1991) only for *Homostius* and *Buchanosteus* agrees with the synapomorphies retained in the phylogeny (Fig. 14). The monophyly of the Eubrachythoraci, supported by four synapomorphies, will probably be maintained when pachyosteomorph taxa will be added to this analysis.

The taxon Migmatocephala, erected by WHITE (1972), includes *Antineosteus*, *Homostius*, *Tæmasosteus*, *Tityosteus*, and *Arenipiscis* (see comments above), but not *Buchanosteus* as envisaged by WHITE, because its phylogenetic position is not fixed according to the discussed phylogenetic analysis. Although *Goodradigbeeon*, was not analysed here, it shares the same morphological pattern of the inferognathal plate as *Antineosteus* and, consequently, could be included in the Migmatocephala. The characters used by WHITE (1972: 381) to characterize the Migmatocephala (*i.e.* separate rostropineal plate, short preorbital plates with complete medial contact, orbit large and directed obliquely forward), are not retained as synapomorphies for this clade, but rather interpreted as plesiomorphic features or not coded in the matrix. CARR (1991) gave a diagnosis of the 'primitive brachythoracids' in which one synapomorphy is shared with the present analysis: the long paranuchal and nuchal plates. The character (53) does not support the monophyly of Migmatocephala, while it appears in CARR's analysis as a synapomorphy (character 82). This discrepancy is explained by the fact that the taxa coded are not the same and because of the different coding. I consider *Buchanosteus* as plesiomorphic for this character. CARR's character 31 is not coded in my analysis. In the present analysis, the Eubrachythoraci includes *Holonema* (Fig. 14). This conclusion differs from CARR's phylogeny (1991, see Fig. 20B, D), and this phylogenetic position of *Holonema* explains the differences between the two diagnosis for the Eubrachythoraci. The monophyly of the coccosteomorph arthrodires (CARR, 1991) [camuropiscids + [*Coccosteus cuspidatus* + *Incisoscutum*]] (Fig. 14), is supported by six synapomorphies of which two are shared in both analysis, characters 10 [1] and 15 [1].

The presence of *Holonema* as the most primitive Eubrachythoraci is argued for by four synapomorphies and implies the interpretation of some characters as homoplastic features while they are commonly used to argue for the phylogenetic position of *Holonema* as a primitive brachythoracid. These characters are: the absence of a carinal process on the median dorsal plate (character 40[0]), the occurrence of a large submarginal plate (character 26[0]), the co-ossified palatoquadrate (character 15[0]), and a long thoracic armour. One stress the fact that some of this characters are functional. *Maideria* is the most primitive brachythoracid but it is incompletely known. Some characters are interpreted as homoplastic such as the development of a long snout. This feature was known until now in the Late Devonian Eubrachythoraci from Gogo (Australia) and Wildungen (Germany). The occurrence of the ventral sensory line on the anterior ventrolateral plate is retained as the only uniquely shared derived feature to place *Maideria* as the sister-taxon of Eubrachythoraci, this phylogenetic position occurs in only one of the topologies (Fig. 13B).

Coccosteomorph arthrodires including camuropiscids, *Incisoscutum*, and *Coccosteus cuspidatus* are monophyletic, but an analysis including *Eastmanosteus calliaspis*, plourdosteids or torosteids, Moroccan dunkleosteids, *Dunkleosteus terelli* and pachyosteomorphs (aspinothoracid arthrodires) will be a test for some of the synapomorphies considered in this analysis (Fig. 14).

POSSIBLE EVOLUTIONARY TRENDS WITHIN BRACHYTHORACIDS

Placoderms are known from the Middle Silurian (GOUJET, pers. comm. on Chinese material). Brachythoracids appeared as early as the Emsian in the Gondwana (Morocco, Iran and Australia) where they are both dated by conodonts. Among placoderms, brachythoracids are considered as the most derived and diversified group. They have their youngest representatives in the Famennian. For a very long time brachythoracids were considered to be homogenous, but some authors nevertheless recognised a mosaic evolution, in contrast MILES (1969) considered brachythoracids as 'a valid evolutionary group even though the differences between them in the development of the trunk shield are not always clear-cut'. Evolutionary trends within brachythoracids are proposed considering the most recent phylogenetic analyses (YOUNG, 1981; GARDINER & MILES, 1990; CARR, 1991).

Evolutionary trends relative to the skull-roof are most difficult to trace by comparison to the variable pattern of the Migmatocephala and the more stable one of the Eubrachythoraci. The posterior part of the skull-roof is constrained to a greater stability when a posteriorly broad and thick nuchal region has been developed in connection with the development of a dermal articulation, and the long nuchal and paranuchal plates have been lost. This region is strengthened by a complete nuchal thickening within the Eubrachythoraci, but a variation occurs as to the disposition of the nuchal pits on the ventral surface of the nuchal plate, and the development of the concavity of the posterior margin of the skull-roof.

The prenuchal part of the skull-roof exhibits the most variable pattern, and several of them may be described. The presence of a rostropineal plate occurs in buchanosteids (*Buchanosteus* and *Errolosteus*) and in *Arenipiscis*, according to (YOUNG, 1981, Fig. 5). The rostral plate is primitively wide, as in *Antineosteus* and then tends to become triangular shape as in the Eubrachythoraci. A rostropineal plate is known to date only in Australian or Gondwanan brachythoracid taxa.

The orbits are primitively anteriorly placed in the Migmatocephala, whereas they face laterally in the Eubrachythoraci, the lateral position is not retained as a synapomorphy, contrary to LELIÈVRE (1984a, 1988). The composition of the dorsal orbital margin changes as well. In the outgroups and the Migmatocephala, the dorsal orbital margin is composed by three or more plates, including the postnasal, preorbital and postorbital plates. In the Eubrachythoraci, only the preorbital and the postorbital plates constitute the dorsal margin of the orbit; the postnasal plates are situated in a more anterior position, together with the anterior nostrils. One can associate this pattern with the resorption of the ethmoidian fissure and its replacement by a blood vascular plexus, related to the pineal plate pattern, the course of the medial contact between the preorbital plates, and the more anteriormedial position of the nasal capsules (see comments p. 175-176). The development of the suborbital lamina of the suborbital plate is more pronounced in

the Eubrachythoraci because of the lateral position of the orbits, while it is short in the Migmatocephala because of the more anteriorly located orbits. The remodelling of this region and, mainly, the displacement of the postnasal plates in a more anteromedial position implies a contact between the suborbital and the preorbital plate. This contact was between the suborbital and postnasal plates in the Migmatocephala and *Buchanosteus*. This latter disposition is retained in camuropiscids. One exception to this general scheme is given by the autapomorphic pattern of *Homostius*.

A closed angle (less than 90°) between the two branches of the infraorbital sensory line on the suborbital plate, considered as a synapomorphy of the Migmatocephala (LELIÈVRE, 1984a, 1988), does not support any monophyletic group. A tendency towards the disappearance of the supraoral sensory line is observed in pachyosteomorph.

The development of the ventral structures of the skull-roof in Eubrachythoraci increases, compared to their relative importance in Migmatocephala. It is the case for the lateral consolidated region and the development of the supraorbital vault; these characters were not coded here, but by CARR (1991: 381).

For a long time, the trilobate central plates have been considered as diagnostic of the 'coccosteids'. CARR (1991: 379) has shown the ambiguity of this term, and proposed to subdivide this character into three discrete characters, among which the presence of an embayment for the preorbital plate in the central plate is a synapomorphy of the clade [camuropiscids + [*Coccosteus cuspidatus* + *Incisoscutum*]] or of the clade 'coccosteomorph arthrodires' of CARR (1991).

Even though the gnathal elements of the Migmatocephala are imperfectly known, their inferognathal seem to exhibit such plesiomorphic features as the presence of many denticles and a blade portion opened ventrally. It would be astonishing if new discoveries of gnathal elements of the Migmatocephala differ fundamentally from this plesiomorphic type, which consists of gnathal elements with many denticles, as found in *Goodradigbeeon* and *Antineosteus*. This trend is supported by one of the four synapomorphies diagnosing the Eubrachythoraci: the absence of denticles of the anterior superognathal plate, and also by the occurrence of a dorsal process on the anterior superognathal plate, which supports the monophyly of the basal clade [camuropiscids + [*Coccosteus cuspidatus* + *Incisoscutum*]].

The thoracic armour of the Migmatocephala reveals different patterns. The pectoral fenestra is either open (e.g. *Antineosteus* and *Homostius*) or closed in *Buchanosteus*. The former disposition is linked to a short thoracic armour, with a developed condyle on the anterior dorsolateral plate and a short median dorsal plate bearing ventrally a keel and a pronounced unexcavated carinal process. A posteriorly excavated process is constant in coccosteomorphs and pachyosteomorphs wether or not the median dorsal plate is long; however it occurs also in *Buchanosteus* and *Maideria*. The position of *Holonema* shows that this functional character defined on the median dorsal plate could be absent of the diagnosis of the basal Eubrachythoraci clade.

The loss of the posterior median ventral and posterior ventral plates is a synapomorphy of *Antineosteus* and *Homostius* (may be also *Tiryosteus*). It is associated with both short median dorsal plate and lateral wall of the thoracic armour.

Two dispositions occur for the spinal plate. A short spinal plate (the pseudospinal plate of MILES & DENNIS, 1979; see also GARDINER & MILES, 1990: 198) lacking a lateral process and an internal spinal pit, is found in *Homostius*. Another disposition occurs in *Buchanosteus*, in

which the spinal plate is long and straight according to WHITE & TOOMBS (1972); however nothing is known about the internal surface of this plate. This disposition is the spinal structure retained as plesiomorphic by GARDINER & MILES (1990) for *Coccosteus*, *Plourdosteus*, *Harrytoombsia* and *Torosteus* for instance. Reduction and transformations of the spinal plate may well have occurred several times; thus, phylogenetic trends are difficult to trace, except for the absence of the lateral pectoral process in brachythoracids. Some brachythoracid genera have an anterior lateral plate with a high dorsal lamina, a synapomorphy uniting *Buchanosteus* with the Migmatocephala. Other characters of the thoracic plates, such as the development of the apron, have been discussed by WHITE (1952). His conclusion does not take into account the anterior orientation of the ventral lamina of the interolateral plate and of the branchial space. Character 41 deals with the development of the ventral lamina of the interolateral plate, together with the occurrence of an ornamentation. The presence of the ornamentation is derived for Eubrachythoraci and Migmatocephala, but the development of the ventral lamina, which remains short in *Coccosteus cuspidatus*, as well as in the Migmatocephala, is parallely derived. While *Holonema*, camuropiscids and *Incisoscutum* share a large ventral lamina.

The Migmatocephala is a clade, characterized by a particular morphological design of the skull-roof. The earliest record of this taxon is Emsian, while the youngest record is probably from the Lower Givetian, with *Homostius* as the youngest known genus, and described only from Laurasia (Scotland, Estonia and Canada). There is no representative during the Middle Devonian in the Gondwana, but the clade is the most diversified in Australia, where the oldest record is found.

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TABLE 1. — Data matrix of 53 characters for 12 taxa. *Arenipiscis*, while not taken into account in the interrelationships of brachythoracids, is coded in the data matrix. [0] = plesiomorphic state, [1-2] = apomorphic states, [?] = character state missing. Synapomorphies (CI = 1.000) are indicated in bold.

*Matrice de données de 53 caractères pour 12 taxa. Le codage des caractères d'*Arenipiscis *est donné bien que ce taxon n'ait pas été pris en compte dans l'analyse des relations de parentés des Brachythoracii. [0] = état plésiomorphe, [1-2] = états dérivés, [?] = caractère non observé. Les synapomorphies dont le CI = 1.000 sont indiquées en gras.*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Dicksonosteus	**0**	**0**	**0**	0	1	**0**	0	0	**0**	0	**0**	**0**	0	**0**	**0**	**0**	0	0	0	0	0	0	**0**	0	0	0	1	**?**
Arctolepis decipiens	**0**	**0**	**0**	0	1	**0**	?	0	**0**	**0**	**0**	**0**	0	0	**0**	**0**	0	0	2	0	0	0	0	?	0	0	1	**0**
Antineosteus	**1**	**?**	**0**	0	1	**1**	2	2	**0**	**0**	**1**	**1**	1	0	**?**	**0**	1	0	0	1	1	?	0	1	0	1	0	**?**
Homostius	**1**	**?**	**0**	0	1	**1**	2	2	**0**	**0**	1	**1**	1	0	**?**	**0**	1	0	2	0	1	?	N	0	0	1	1	**?**
Buchanosteus	**1**	**1**	**0**	?	?	**1**	1	2	**0**	**0**	**0**	**1**	1	1	**0**	**0**	1	**0**	0	0	1	0	0	1	**0**	1	1	**?**
Holonema	**1**	**1**	**0**	0	0	**1**	2	0	**1**	**0**	**0**	**1**	1	0	**0**	**1**	2	1	2	0	0	**0**	1	0	0	0	0	**0**
Tæmasosteus	**1**	**?**	**?**	?	?	**1**	1	2	**0**	**0**	**1**	**1**	**0**	1	**?**	**0**	0	0	?	?	1	?	?	**0**	?	1	?	**?**
Arenipiscis	**1**	**?**	**?**	?	?	**1**	1	2	**?**	**?**	**1**	**1**	?	?	**?**	**0**	0	0	0	**0**	1	**0**	1	1	0	?	?	**?**
camuropiscids	**1**	**1**	**2**	1	0	**1**	1	2	**2**	**1**	**0**	1	0	1	**1**	**1**	1	1	1	0	0	0	1&2	1	1	2	1	**1**
Coccosteus cuspidatus	**1**	**1**	**0**	2	0	**1**	1	1	**2**	**1**	**0**	1	0	1	**1**	**1**	2	0	2	1	1	1	1	0	1	1	1	**1**
Incisoscutum	**1**	**1**	**0**	1	0	**1**	1	1	**2**	**1**	**0**	1	0	1	**1**	**1**	1	1	2	1	0	1	2	1	1	1	1	**1**
Maideria	**1**	**1**	**1**	1	1	**1**	0	1	**0**	**0**	**0**	**0**	?	?	**?**	**0**	1	1	0	0	1	0	2	0	1	?	?	**0**
Tityosteus	**1**	**1**	**0**	2	0	**1**	?	2	**0**	**0**	**1**	**1**	1	1	**?**	**0**	1	0	2	0	1	1	0	?	0	?	?	**?**

	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53
Dicksonosteus	?	**?**	0	**0**	0	**0**	**0**	**0**	**0**	**0**	0	**0**	0	0	0	0	**0**	0	**0**	**0**	0	**0**	**0**	0	0
Arctolepis decipiens	0	**0**	?	**0**	?	**0**	**0**	**0**	**0**	**0**	**0**	0	0	**0**	0&1	0&1	0	0	**0**	**0**	0	**0**	**0**	0	0
Antineosteus	?	**?**	1	**0**	0	1	**?**	1	**0**	1	1	1	1	1	0	0	1	1	**0**	**2**	0	**0**	**0**	1	0
Homostius	?	**?**	1	**0**	1	1	**1**	1	**0**	1	1	1	1	1	0	0	1	1	**0**	**2**	0	**0**	**0**	0	1
Buchanosteus	?	**?**	?	**?**	?	0	**1**	**0**	**?**	**0**	0	2	1	1	0	1	1	1	**0**	**0**	0	**0**	**0**	1	0
Holonema	0	**1**	0	**0**	?	0	**1**	**0**	**0**	**0**	1	0	2	0	1	1	1	1	**1**	**1**	1	**0&1**	**0**	0	0
Tæmasosteus	?	**?**	?	**?**	?	?	**?**	**?**	**?**	1	1	1	1	1	?	1	1	1	**0**	**0**	?	**0**	**0**	1	1
Arenipiscis	?	**?**	?	**?**	?	?	**?**	**?**	**?**	1	1	1	?	1	1	0	1	?	**?**	**1**	?	**0**	**0**	?	?
camuropiscids	2	**1**	1	**1**	1	0	**1**	**0**	**1**	**0**	1	2	2	**0**	0	1	1	1	**1**	**1**	1	**0&1**	**0**	0	0
Coccosteus cuspidatus	2	**1**	1	**1**	1	0	**1**	**0**	**1**	**0**	0	2	1	0	0	1	0	0	**1**	**1**	1	**1**	**1**	1	0
Incisoscutum	1	**1**	1	**1**	1	1	**1**	**0**	**1**	**0**	1	2	2	0	0	1	0	0	**1**	**1**	1	**0**	**0**	0	0
Maideria	1	**0**	?	**?**	?	?	**?**	**0**	**?**	**0**	0	2	?	0	1	1	1	?	**?**	**0**	1	**0**	**0**	?	?
Tityosteus	?	**?**	?	**?**	?	1	**?**	**?**	**0**	1	1	?	?	1	0	1	1	?	**?**	**2**	?	**?**	**0**	?	?

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Plicatodus jordani n. g., n. sp., a new xenacanthid shark from the Lower Permian of Europe (Saar-Nahe Basin, Germany)

by Oliver HAMPE

(A contribution to IGCP 328-Palaeozoic Microvertebrates)

Abstract. — By means of a partial anterior skeleton within a nodule, a new xenacanthid shark, *Plicatodus jordani* n. g., n. sp., is described from the Lower Permian of the SW-German Saar-Nahe Basin. Its tricuspidate teeth show wavy cristae of hybodontoid pattern, and an extremely flattened base with a coronal button, histologically made of orthodentine. These characteristics are different from the currently known xénacanthid genera. The Bohemian "*Orthacanthus*" *plicatus* belongs to the same genus and is reviewed here. A cladogram of the order Xenacanthida is given, based only on hard parts, using ctenacanthids for outgroup comparison.

Keywords. — Vertebrata, Chondrichthyes, new taxon, Lower Permian, Germany, anatomy, phylogeny.

***Plicatodus jordani* n. g., n. sp., un nouveau xénacanthe du Permien inférieur d'Europe (bassin de la Sarre, Allemagne)**

Résumé. — Un nouveau requin Xénacanthide, *Plicatodus jordani* n. g., n. sp., du Permien inférieur du bassin de la Sarre (sud-ouest de l'Allemagne) est décrit à partir de la partie antérieure fragmentaire d'un squelette contenu dans un nodule. Ses dents tricuspides présentent des crêtes ondulées semblables à celles des Hybodontoïdes, et une base très aplatie portant un bouton coronal formé d'orthodentine. Ces caractères diffèrent complètement de ceux que l'on connaît des autres genres de Xénacanthides. «*Orthacanthus*» *plicatus* de Bohème est révisé et attribué à ce nouveau genre. Enfin un cladogramme de l'ordre des Xenacanthida est proposé ; il est construit sur les seuls caractères des dents et des épines, et utilise les Cténacanthides comme groupe extérieur pour la comparaison.

Mots-clés. — Vertebrata, Chondrichthyes, nouveau taxon, Permien inférieur, Allemagne, anatomie, phylogénie.

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INTRODUCTION

The Xenacanthida are a fossil order of elasmobranchs of predominantly Paleozoic age, which very successfully adapted to freshwater. Their remains are known from many sites in the world. They occur in North America (e.g. HOTTON, 1952: Texas; LUND, 1975: Appalachians; MASSON & RUST, 1984: Canadian Atlantic Provinces), Europe (e.g. HAMPE, 1989: Germany; FRITSCH, 1889: Bohemia; HEYLER & POPLIN, 1989: France; AGASSIZ, 1843: UK; HEINTZ, 1934: Norway; SOLER, in litt.: Spain; SCHNEIDER, pers. observ.: Ukraine), South America (WÜRDIG-MACIEL, 1975: Brazil); India (JAIN, 1980) and Australia (TURNER, 1982).

The SW-German Saar-Nahe basin consists of Upper Carboniferous and Lower Permian fluvio-lacustrine deposits which are very rich in xenacanthid material. It is the largest Permo-Carboniferous molasse basin within the Variscan orogenic chains (SCHÄFER, 1989) in Central Europe. Surface access is possible within an area of 100 × 40 km just south of the Renish Schiefergebirge. Within the Saar-Nahe Basin isolated teeth and many articulated skeletons are distributed in over one hundred localities of lacustrine and deltaic environments.

The main characteristics of xenacanthid sharks are: an elongated dorsal fin extending from directly behind the shoulder girdle to the level of the usually diphycercal caudal fin, from which it is separated by a notch; the skeleton of the pectoral fins shows a long segmented central axis with radials diverging from both the pre- and postaxial borders ("archipterygium"-type); all xenacanthids possess a dorsal spine, which articulates with the neurocranium or can be placed in its back in the neighbourhood of the shoulder girdle (KNER, 1867; FRITSCH, 1889, 1895; JAEKEL, 1906; ZANGERL, 1981; HEIDTKE, 1982; KLAUSEWITZ, 1986, 1987; ZIDEK, 1988; POPLIN & HEYLER, 1989).

Xenacanthids are often recognized by their distinctive dentition. Their teeth have a tricuspid crown with two lateral main cusps and an often distinctly smaller and more delicate median cuspule. The base is drawn out lingually and bears a coronal button on its top and a basal tubercle on its bottom side. Comprehensive investigations of teeth of the genera *Orthacanthus*, *Xenacanthus* and *Triodus* are given by HAMPE (1988a, b; 1989; 1991). The terminology used in this article is based on these papers.

A recently discovered nodule from the "Lebacher Toneisensteinlager" (found at the University of Leipzig by SCHNEIDER) shows a partial cranial skeleton of a xenacanthid (including parts of the palatoquadrate, mandible, branchial skeleton, shoulder girdle, spine fragment) with teeth having some features totally different to the known genera.

FRITSCH (1889) described an isolated tooth from the Stephanian B from Bohemia under the name *Orthacanthus plicatus*. Only a few additional teeth of this kind were subsequently collected from boreholes of approximately the same stratigraphic level (ZAJÍC, pers. comm.).

The Bohemian teeth and the SW-German nodule belong to a new genus called *Plicatodus*. This paper deals with the presentation of the species *P. jordani* (n. sp.; Germany) and *P. plicatus* (Fritsch; Bohemia).

ABBREVIATIONS

ang	angle between crown and base in lateral view, *angle entre la couronne et la base en vue latérale*;
bs	base, *base*;
bt	basal tubercle, *tubercule basal*;
cb	coronal button, *bouton coronal*;
cbr	ceratobranchials, *cératobranchiaux*;
chy	ceratohyale, *cératohyal*;
cr	crown, *couronne*;
dep	basal depression of basal tubercle, *dépression basale du tubercule basal*;
gd	gill denticles, *denticules branchiaux*;
lc	lateral cusps, *cuspides latérales*;

man	mandible (Meckel's cartilage), *mandibule (cartilage de Meckel)*;
mc	median cuspule, *petite cuspide médiane*;
na	neural arches, *arcs neuraux*;
nf	nutrient foramina, *foramina nourriciers*;
pc	pulp cavity of spine, *cavité pulpaire de l'épine*;
pq	palatoquadrate, *palatocarré*;
sc	scapulocoracoid, *scapulocoracoïde*;
sh	lingual shaft of coronal button, *prolongement lingual du bouton coronal*;
sp	spine, *épine*;
tpr	tongue-shaped process of the base, *processus linguiforme de la base*;
va	ventral arches, *arcs ventraux*;
vc	vertical cristae, *crêtes verticales*.

BAF	Bergakademie Freiberg, Germany;
GPL	WB Geophysik, University of Leipzig, Germany;
NMVP	Národní Muzeum of Prague, Czech Republic;
UUG	Ustrední ústav geologicky, Prague ("Geological Survey"), CZ.

MATERIAL AND METHODS

The relatively poor material of the new taxon *Plicatodus* (low number of teeth) was investigated at the National Museum in Prague and at the Bergakademie in Freiberg/Saxony. The Lebach-nodule was lent from the University of Leipzig. All material was compared with the diverse and rich xenacanthid fauna from the Upper Carboniferous and Lower Permian deposits of the Saar-Nahe and Bohemian basins.

The documentation of the anterior skeleton, which is the only persistent part within the nodule, was supported by X-ray examination.

The histological structure of the teeth of *Plicatodus jordani* is shown by application of fluorescence microscopy. For this method no thin sections, but only cuts with a polished surface of the objects are needed to analyze them under incident light.

Fluorescence microscopy uses transmitted light and, in particular, incident light for the excitation of fluorescence radiation. If an object is irridiated by short-wave excitation light, fluorescing substances will emit light of specific colors, while the non-fluorescing background remains dark. Suitable excitation filters are used to select those wavelengths which cause fluorescence exactly out of the light coming from the source. All other wavelengths which do not contribute to the fluorescence in question are cut off by barrier filters. For this investigation an excitation with blue light (range 420-490 nm) was used.

Polished sections of teeth, prepared out of the replacement battery of the nodule, were made in the following way: single teeth were embedded in bio-resin; then the object was cut and during repeated grinding-down a series of cuts after the principle of tomography had been obtained (for detailed information to this procedure, see HAMPE, 1991).

All investigations were carried out using a research microscope with an incident light fluorescence illuminator, equipped with filtercube devices, halogen lamp and automatic camera.

The vascularization system is documented by the existence of broken teeth or by mechanically cut material.

SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Order XENACANTHIDA Glikman, 1964
Family XENACANTHIDAE Fritsch, 1889
Genus **PLICATODUS** n. g.

TYPE SPECIES. — *Plicatodus jordani* n. g., n. sp.

DIAGNOSIS. — Dorsal spine, laterally equiped with a single row of denticles, which articulates with the occipital region of the head; tricuspidate teeth; crown wearing curved or wavy, sometimes splitted vertical cristae (hybodontoid pattern); often extremely flattened base; rounded coronal button on the upperside of the base; rhomboid or rounded basal tubercle with depressed socket on the bottom side.

ETYMOLOGY. — After the peculiar pattern of cristae on the teeth (lat.: *plica* = crease).

REMARKS. — Several characteristics of *Triodus* and *Xenacanthus* are combined within the genus *Plicatodus*.

Plicatodus shares wide lumina of the pulp cavities and vertical cristae bearing cusps with *Triodus*. However, the hybodont-like pattern of the cristae is different from that of *Triodus*. Generally common between *Xenacanthus* and *Plicatodus* are the flattened base, the large number of nutrient foramina and the often relatively small and flat coronal button. The cusps of most *Xenacanthus* species have lanceolate cross-section, which are only slightly indicated in *Plicatodus*.

REFERRED SPECIES. — *Plicatodus plicatus* (Fritsch, 1889), Stephanian B of Bohemia/CZ; *Plicatodus jordani* n. sp., Lower Rotliegend of the Saar-Nahe Basin/SW-Germany; (?) *Plicatodus santosi* (Würdig-Maciel, 1975), Upper Permian of Porto Alegre/Brazil.

Plicatodus jordani n. sp.
(Figs. 1-5)

1988 *Xenacanthus plicatus* A. Schneider: 74, Figs. 3,7, 4; Pl. I, Fig. 11.

DIAGNOSIS. — A species of the genus *Plicatodus* with following characteristics: dorsal spine which articulates with the neurocranium, having rows of denticles situated on its lateral faces. Teeth with a height of 1-3.5 mm; cross-section of cusps near the base elliptical, closer to the tip polygonal (cristae!); height of median cusp reaching 1/2 to 1/3 that of lateral cusps; lateral cusps having between 4 and 10 partly wavy or curved vertical cristae (hybodont pattern); outline of the base rounded with a mesio-distal extent; flat and rounded, sometimes rhomboid coronal

button with short suggested shaft; about 16 nutrient foramina on the upperside of the base; bottom side showing a rhomboid-shaped or rounded basal tubercle with basal depression and 7-15 nutrient foramina; angle between crown and base in lateral view about 100°; vascularization system consists of a wide pulp cavity below the crown and lingually positioned anastomosing nutrient canals; crown and base, including coronal button constructed of orthodentine; no enameloid tissue developed.

HOLOTYPE. — GPL 3828a, b, nodule (original plus counterpart) including a partial anterior skeleton.

TYPE LOCALITY. — "Lebach" (probably from Rümmelbach-Gresaubach area), Saar-Nahe basin.

TYPE HORIZON. — "Lebacher Toneisenstein-Lager" = Humberg-Bank, Uppermost Lauterecken to Odernheim-Schichten (L-O10, after BOY & FICHTER, 1982), Lower Permian.

ETYMOLOGY. — In honor of the famous H. JORDAN, who had collected and described many fossils of the "Lebacher Toneisenstein-Geoden" in the last century.

DESCRIPTION

The specimen is preserved within a nodule from the famous "Lebacher Toneisenstein-Lager", where hundreds of that kind had been collected during last century. The diameter of the geode is approximately 14 × 9 cm.

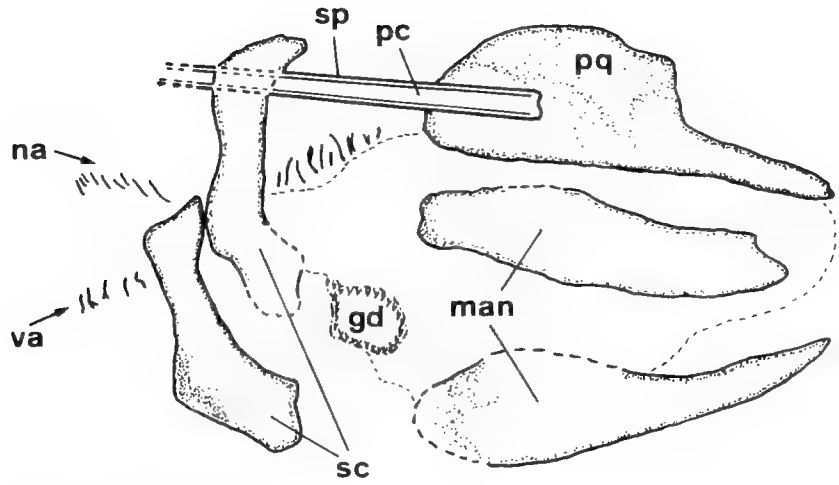
In GPL 3828a are observed the left mandible, the surface of the right quadrate region and mandible, the shoulder girdle, the spine which is partially covered with matrix, and some neural and ventral arches (Fig. 1). The replacement teeth of the right mandible can be seen in basal view. Behind the jaws, there is also a small area with accumulated gill denticles. Each has a height of about 1-2 mm and mainly consists of two crescent-shaped curved cusps (Fig. 3b) and a base with some large nutrient foramina and a peg-shaped extremity.

The counterpart (GPL 3828b) shows the right upper and lower jaw, the impression of the left mandible, a partial shoulder girdle, the distal portion of the spine, branchial arches, and teeth of the right palatoquadrate in lingual view (Fig. 2). Some of the information was supported by radiograph observation.

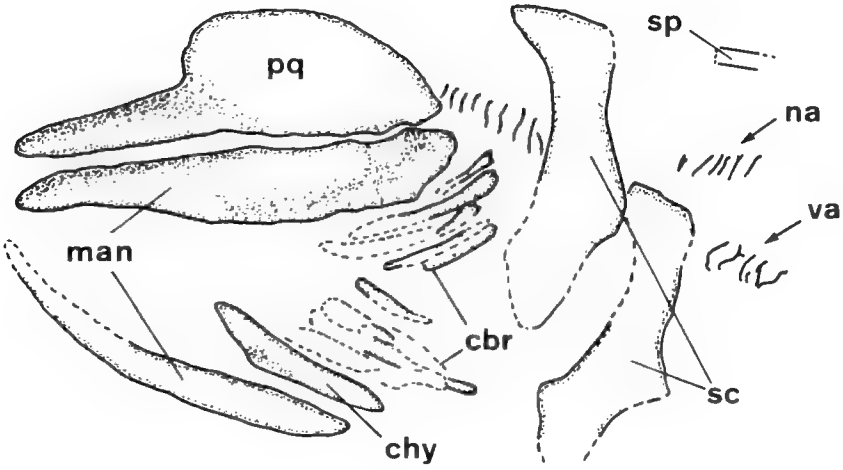
HEAD

The neurocranium is situated deep in sediment. No exact outlines are visible. The cleaver-shaped, slightly damaged palatoquadrate has an anterior palatine region (pars palatina) and a posterior quadrate region (pars quadrata) in which the fairly crushed palatine region seems to be relatively thin. The quadrate is elevated behind the orbit at 1/3 of the height of palatine portion. Its anterior border forms the hind margin of the orbit. The posterior margin is convex and curves gently backwards and downwards. Generally the outlines are not very well documented. The knob-like articular process is partially covered and not clearly in view.

The much more massive mandible (Meckel's cartilage) becomes reduced in height in the anterior part, ending like a stem. The posterior half is excavated ventrally on the internal side to form a fossa; leaving the ventrolateral edge standing out at the external side as a ridge upon



GPL 3828 a



GPL 3828 b

FIG. 1. — *Plicatodus jordani* n. g., n. sp., GPL 3828a and b, holotype. Partial anterior skeleton from the nodule of the "Lebacher Toneisenstein-Lager", Lower Rotliegend (L-O10), Saar-Nahe Basin. Abbreviations, see text. The length of the spine, drawn above, corresponds with 6 cm.

Plicatodus jordani *n. g., n. sp., GPL 3828a et b, holotype. Partie antérieure du squelette provenant du nodule de la "Lebacher Toneisenstein-Lager", Rotliegend inférieur (L-O10), bassin de la Sarre. Abréviations, voir texte. La longueur de l'épine dessinée au-dessus est de 6 cm.*

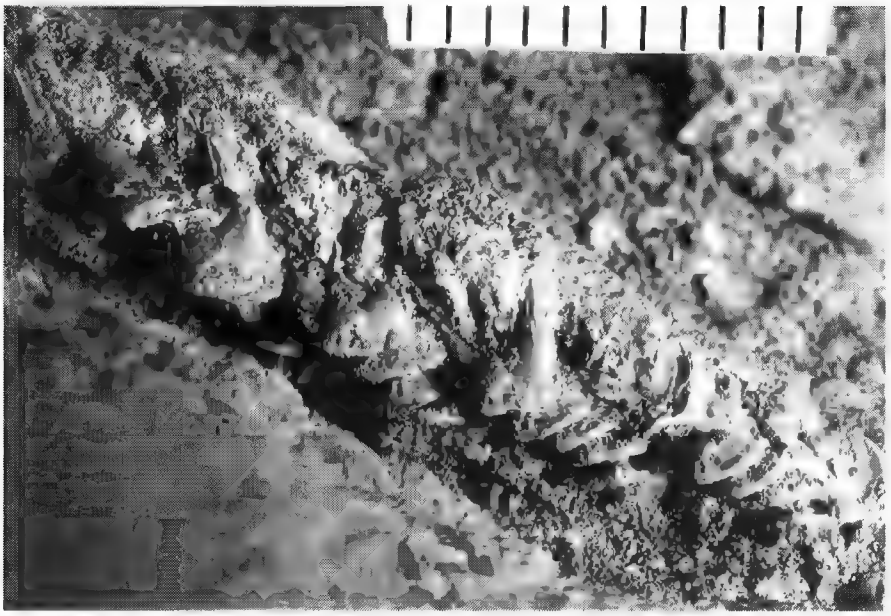


FIG. 2. — *Plicatodus jordani* n. g., n. sp., GPL 3828. B, holotype. Replacement teeth of the right palatoquadrate in lingual view. Scale bar with intervals of 1 mm.

Plicatodus jordani *n. g., n. sp., GPL 3828. B, holotype. Dents de remplacement du palatocarré droit en vue linguale. Graduations de l'échelle : 1 mm.*

which the M. adductor mandibulae inserted during life. The very posterior part, including the articular region of the mandible, is crushed.

Of the hyoid arch, only the left ceratohyale in GPL 3828b is preserved. It shows an outline like that of the mandible.

The branchial skeleton consists of five arches, but there is no clear division or separation into the single elements. Probably these are the ceratobranchials.

POSTCRANIAL SKELETON

The pectoral girdle is formed by a pair of large leaf-like scapulocoracoid cartilages which can be observed quite well. They have a typical xenacanthid morphology showing two flexures: a lower one separated the coracoid part (in this level the posterior directed articular crest for the pectoral fin can be found), and an upper one. In both halves of the nodule, a row of neural arches is situated dorsally between head and scapulocoracoids and behind the shoulder girdle. Ventral arches are only behind shoulder girdle.

SPINE

The dorsal spine, a main characteristic of xenacanthid sharks, resembles that of genus *Triodus* which has a row of denticles on each lateral side. The large pulp cavity has normal pro-

portions: the diameter of the cavity in the middle and most proximal regions is about 1/2 and 4/7 as long as the average cross-section respectively. The overall length of the spine can be estimated at greater than 8 cm.

TEETH

The teeth of this newly defined species have a height between 1 and 3.5 cm. Their median cusp reaches about 1/2 to 1/3 that of the lateral cusps. In cross-section the cusps are elliptical near the base and become polygonal towards the apical direction. The upper part of the distal cusp has a sigmoidal curvature, visible from the lingual and labial side. The sculpture of the cusps consists of 4 to 10, sometimes splitted, cristae. In part, the vertical cristae have a wavy, S-shaped form, very similar to that known in hybodont sharks; sometimes they run nearly straight. The cristae originate at the tip and occupy the upper 3/4 of the cusps.

The base shows a discus-like character: fairly flat, connected with mesio-distal extension. A tongue-shaped process is located at the distal pointed curvature of the base. It is separated by a lingually positioned indentation (Fig. 3d).

On the upper side, a flat, rounded, sometimes rhomboid coronal button is situated which also can have an oviform outline in labio-lingual extension. A short shaft is indicated. About 16 foramina are irregularly distributed on the upperside of the base.

The bottom side has a rhombic to ovoid and considerably strong basal tubercle with a concave depression. The number of nutrient foramina amounts to about seven larger ones; altogether about 10-15 are possible.

The angle between base and crown in lateral view comes to approximately 100°.

The vascularization system consists of a wide pulp cavity (Fig. 4) below the cusps. From this cavity a wide canal extends into each cusp. In this case, the hard tissues of the cusps developed rather thin. In the median part of the base, the cavity is divided into a low number of large canals crossing through. Multiple nutrient canals with a small internal diameter pass through the base only in the lingual part.

The dentition of *Plicatodus jordani* is distinctly heterodontous. The anterior and posterior teeth are smaller, whereas the laterals have the largest size. The mesial cusp is vertically oriented, often with sigmoidal curvature in its lateral view. The distal cusp is directed distally. One set of teeth include approximately 20-22 tooth families. Within the holotype, five rows of teeth can be identified as being replacements.

Commissurals of different morphology are known (Fig. 3c). Their height extends to 1 mm.

The crown bears only two cusps, each showing about 3-4 cristae. Only 2 nutrient foramina are situated on the upperside of the base. The coronal button is very small and has a narrow, lingual shaft. There is nothing yet known concerning the bottom side of the commissurals.

HISTOLOGY

The teeth of *Plicatodus jordani*, crown as well as the base, consists almost entirely of orthodentine (Fig. 5a), like in *Triodus* (see HAMPE, 1991), circumpulpously developed, fluorescing in light yellow and brownish colors. The design of the dentinal tubules can be demonstrated

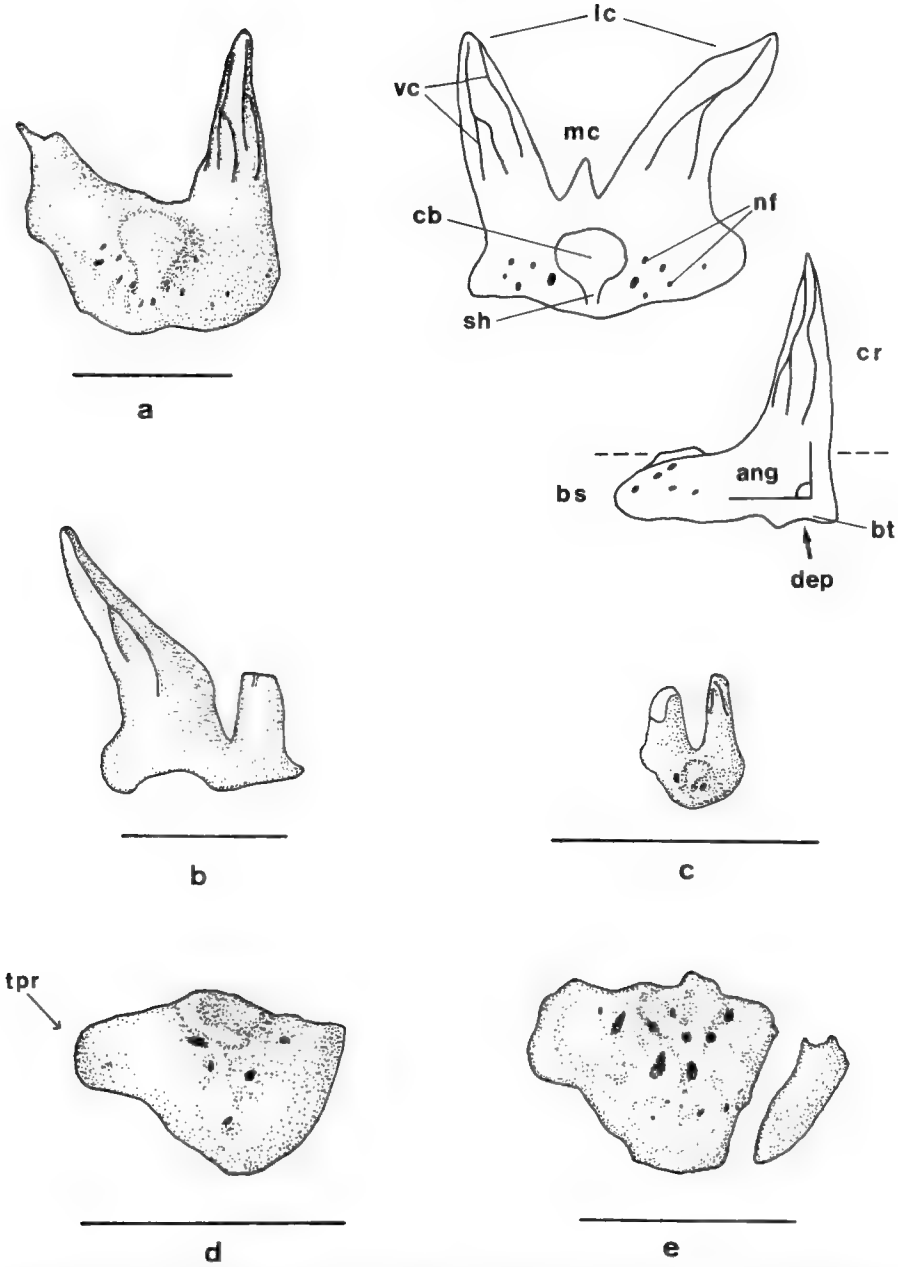


FIG. 3. — Teeth of *Plicatodus jordani*. A, GPL 3828b, lingual view. B, GPL 3828b, labial view. C, GPL 3828b, commissural teeth in lingual view. D, E, GPL 3828a, both in basal view. The figures show only fragmentary teeth; they have been drawn directly from the replacement of the holotype. The schemes in the upper right present the general morphology; for abbreviations, see text. Scales: 2 mm.

Dents de Plicatodus jordani. *A, GPL 3828b, vue linguale. B, GPL 3828b, vue labiale. C, GPL 3828b, dent commissurale en vue linguale. D, E, GPL 3828a, toutes deux en vue basale. Les figures montrent seulement des dents fragmentaires qui ont été dessinées directement à partir du remplacement de l'holotype. Les schémas du haut à droite montrent la morphologie générale ; pour les abréviations, voir le texte. Échelles : 2 mm.*

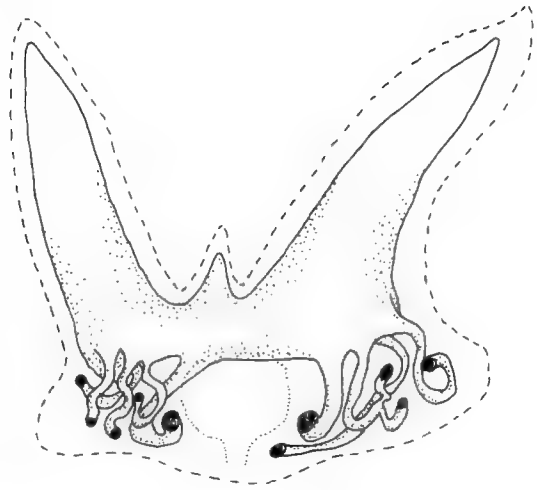


FIG. 4. — Vascularization system of *Plicatodus jordani* in lingual view. The wide pulp canals within the cusps and a large cavity below the crown are characteristic (outline = broken line; coronal button = dotted line).

Système de vascularisation de Plicatodus jordani *en vue linguale. Les larges canaux pulpaires à l'intérieur des cuspides et une vaste cavité pulpaire sous la couronne sont caractéristiques (contour extérieur = tireté ; bouton coronal = pointillé).*

best in horizontal sections of the cusps (Fig. 5b). Near the pulp cavity they are usually arranged in parallel, but show an arborescent embranchment in the outer zones.

In vertical section the material of the relatively flat coronal button looks rather homogeneous. It is suspected, that the button also contains orthodentine (Fig. 5c). An enameloid is absent.

Plicatodus plicatus Fritsch, 1889
(Fig. 6)

1889 *Orthacanthus plicatus* Fritsch: 112; Pl. 88, Fig. 13.
1988 *Xenacanthus plicatus* A. Schneider: 74, Figs. 3, 6; Pl. I, Fig. 10.

HOLOTYPE. — NMVP -M 305, one tooth.

TYPE LOCALITY. — Knezeves near Rakonitz, Bohemia/CZ.

TYPE HORIZON. — "Grauer Schieferton", Kounov member, Upper Stephanian B.

OCCURRENCE. — Stephanian B and C (?) of Rakonitz basin, Bohemia/CZ (see ZAJÍC & STAMBERG, 1985).

DESCRIPTION. — The five investigated teeth are housed in the Národní Muzeum in Prague and in the collection of the Geological Survey of the Czech Republic.

TEETH

Their height is documented between 2.5 and 6 mm. The median cusp reaches 1/4 to 1/3 that of the lateral cusps. Often accessory cuspules can be found beside the median one. The lateral cusps look comparatively massive. They have an elliptical (slightly lanceolate) cross-section. In labial-lingual view the lateral cusps are sigmoidally curved throughout their upper part.

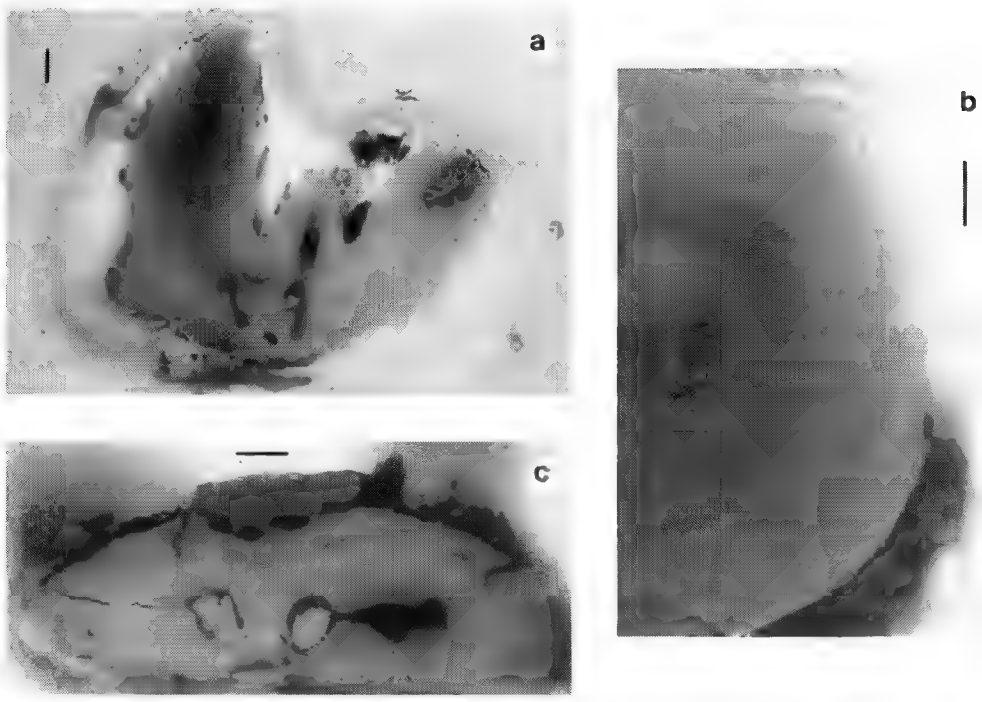


FIG. 5. — Histology of *Plicatodus jordani*. A, vertical section of an entire tooth: crown and base consist of orthodentine with clearly definable growth lamellae (× 43). B, horizontal section of a lateral cusp: in direction to the center (pulp border), the dentinal tubules are arranged nearly in parallel; in the outer zones they show an arborescent embranchment (× 87). C, vertical section through the median part of a base: circumpulpously developed orthodentine with three large central pulp canals and four small nutrient canals below the coronal button. There is no difference ascertainable due to the histological structure of the coronal button (× 70).

Histologie de Plicatodus jordani. *A, section verticale d'une dent entière : la couronne et la base consistent en de l'orthodentine avec des stries de croissance bien définies (× 43). B, section horizontale d'une cuspide latérale : en direction du centre (marge pulpaire), les tubules de la dentine sont disposés presque parallèlement ; dans la zone externe, elles présentent des ramifications (× 87). C, section verticale à travers la partie médiane de la base : orthodentine péripulpaire avec trois grands canaux pulpaires centraux et quatre canaux nourriciers sous le bouton coronal. Il n'y a pas de différence notoire due à la structure histologique du bouton coronal (× 70).*

On the cusps' surface, between 10 and 14 strong and wavy vertical cristae are visible which do not regularly originate at the tip. Generally the cristae cover the entire height of the cusps. This kind of pattern can be noticed in hybodont sharks.

The base is very flat ("pizza") and mesio-distally elongated. The lobe-like shaped mesial edge is often bent downwards (Fig. 6a, c).

The upper side of the base has a small rounded and flat coronal button, sometimes with a short and broad shaft. The number of nutrient foramina cannot be generalized due to the low volume of material, but there could be approximately 10, including one central foramen in front of the median cuspule.

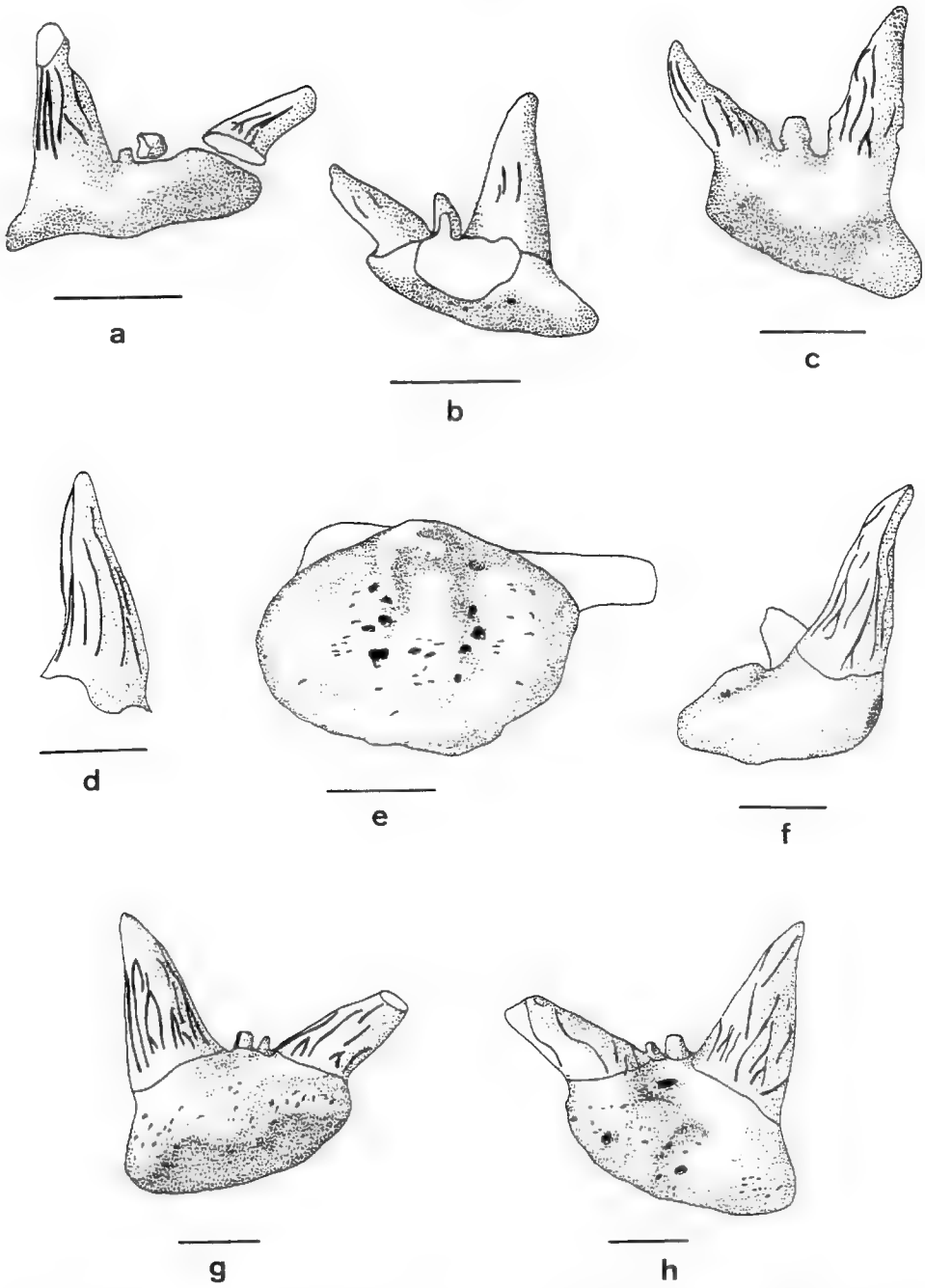


FIG. 6. — *Plicatodus plicatus*, Stephanian B and C (?), Rakonitz basin. A, NMVP-M 305, Knezeves. B, UUG-YA 1370, Nemyslovice. C, UUG-YA 1371, Susno (all in labial view). D, UUG-YA 1372, Meprobylice (separate lateral cusp). E, F, BAF without number, Kounová (basal and lateral aspects). G, H, BAF without number, Kounová (labial and lingual aspects). Scales: 2 mm.

Plicatodus plicatus, *Stéphanien B et C (?), bassin de Rakonitz. A, NMVP-M 305, Knezeves. B, UUG-YA 1370, Nemyslovice. C, UUG-YA 1371, Susno (toutes en vue labiale). D, UUG-YA 1372, Meprobylice (cuspide latérale séparée). E, F, BAF sans numéro, Kounová (vues basale et latérale). G, H, BAF sans numéro, Kounová (vues labiale et linguale). Échelles : 2 mm.*

On the bottom side, a basal tubercle with softly indicated depression is fairly wide labially. On the basal area, about 12 nutrient foramina can be counted. Sometimes these openings are shaped like slots.

The angle between crown and base in lateral view can occasionally be relatively large; regulary it is about 115°.

RESULTS

Generally, cartilage elements of xenacanthids are not very suitable for specific and generic determination within the order (SCHWIND, pers. observ.). On one hand, their morphology is very similar, on the other hand, their outlines depend on the quality of preservation.

The outline of *Plicatodus*' palatoquadrate does not differ from that of *Xenacanthus* or *Triodus*. The general morphology of the upper jaw is considerably similar in all representatives of the family Xenacanthidae. In addition to that, the degree of intraspecific variation, especially of the lower jaw and of the scapulocoracoid, is relatively high, so that these elements should not to be used for species determination.

For comparison, detailed descriptions about the morphology of the cranium and the shoulder girdle are given in the following literature: for *Xenacanthus* and *Triodus* e.g. in FRITSCH (1895), REIS (1897), MOY-THOMAS & WHITE (1939), SCHWIND (1991); for *Orthacanthus* in HOTTON (1952), HEIDTKE (1982), HEYLER & POPLIN (1989).

The proportions of the dorsal spine of *Plicatodus*, which should have been articulated with the occipital region of the braincase, closely resemble that of *Triodus*.

A first description of the teeth from the holotype of *Plicatodus jordani* was briefly outlined by SCHNEIDER (1988) under the name "*Xenacanthus*" *plicatus* A. *P. jordani* shows strong affinities with the Upper Carboniferous, *P. plicatus* from Bohemia.

Both species are characterized by the following features: the strong and hybodont-like pattern of cristae; distal cusps with a sigmoidal curvature in their upper part; a flat, discus-shaped base; relatively small and plain coronal button.

Differences are: *P. plicatus* shows short integral or S-shaped vertical cristae on the entire surface of the cusps, whereas in *P. jordani* the cristae are situated only in the upper 3/4 of the cusps. Furthermore, the base of *P. plicatus* has a downward bent mesial lobe. In contrast to that, *P. jordani* shows a lobe or tongue positioned distally which regularly doesn't bend downwards.

P. plicatus often has accessory median cuspules which lack in *P. jordani*. The concave depression of the basal tubercle is more evident in *P. jordani*.

With "*Xenacanthus*" *santosi* (WÜRDIG-MACIEL, 1975, Pls 8-10; Pl. 15, Figs. 1-4), from the Upper Permian of Brazil, another species belonging to genus *Plicatodus* possibly exists. The cristae on the cusps of the Brazilian teeth are closely similar in number and structure to those of other species of the genus. Their sculpture is only slightly stronger than in *P. jordani*. Also, the cusps are more massive and less slender than in the Bohemian and the SW-German shark.

Differences exist mainly in the morphology of the base. In "*Xenacanthus*" *santosi*, the base is stronger and higher and bears a relatively large and strong coronal button on the upperside. The large number of nutrient foramina corresponds to *P. jordani* and *P. plicatus*.

As opposed to *P. plicatus*, the Brazilian species has a low number of cristae. In *P. plicatus* the cristae are also more weakly developed. A similarity with *P. plicatus* is indicated by the partly slot-like appearence of the nutrient foramina. Moreover, "*Xenacanthus*" *santosi* and *P. plicatus* show a less depressed basal tubercle on the botton side of the base than does *P. jordani*.

Like in all other xenacanthids, *Plicatodus* also lacks an enameloid-like tissue covering the teeth. This is a characteristic feature of this order (see HAMPE, 1991).

Close similarities concerning the histological structure exist with the genus *Triodus*, in having widely luminated vascularization systems within a tooth, entirely constructed of circumpulpously developed orthodentine. In *Plicatodus*, the pulp cavity in the median part of the base is more divided than in *Triodus*, which mostly has only one single cavity. *Plicatodus* shows here a low number of canals. In contrast to this, *Orthacanthus* and *Xenacanthus* have a base made of trabecular dentine and a vascularization system with narrow lumina.

An important characteristic of *Plicatodus* is that the flat coronal button seems to consist of orthodentine, too. In all other genera the coronal button is composed of trabecular dentine. This can be valued as an autapomorphic feature for cladistic analysis (see below).

The structure and distribution of the dentine tubules can be stated as quite individual. Whereas in *Orthacanthus* the tubules are parallel and widely spaced, they are closely spaced in parallel in *Xenacanthus*. *Triodus* has a ramified network. *Plicatodus* shows an arborescent embranchment near the tooth's surface, becoming single and parallel towards the pulp.

CONCLUSIONS

Commonly, the opinion of the vast majority has been that the Xenacanthida are a specialized group of ctenacanthiform sharks. Whereas SCHAEFFER (1981) based his conclusions mainly on neurocranial characteristics, MAISEY (1984) and POPLIN & HEYLER (1989) added several other features, such as spine and fin morphology. However, YOUNG (1982) came to the result that ctenacanthids are more closely related to more derived elasmobranchs than they are to the xenacanthids.

In this article a cladogram is constructed, using the ctenacanthids for outgroup comparison. The scheme includes the genera *Orthacanthus*, *Xenacanthus*, *Triodus* and *Plicatodus* based only on hard parts, because often remnants of calcified and fossilized cartilages are damaged and not easy to reconstruct. In this case, I attach great importance to the suggested cladogram (Fig. 7).

The taxonomic position of DICK's *Diplodoselache woodi*, often placed into the Xenacanthida (e.g. ZANGERL, 1981; SCHNEIDER, 1988; POPLIN & HEYLER, 1989), still remains unclear. Its paired and unpaired fins (pectoral fins with uniserial axial structure like in symmoriids, strongly heterocercal caudal fin), the spine morphology (no denticles visible), and the tooth histology (trabecular dentine within the whole tooth, crown coated with an orthodentine and an enameloid layer, see DICK, 1981) show mainly ctenacanthoid characteristics.

CARROLL (1988) mentioned that *Diplodoselache* is identifiable as a xenacanthid only by its dentition (in this case restricted to the external morphology) and long dorsal fin. Recently GAUDIN (1991) placed *Diplodoselache* into a sister group relationship with xenacanthids.

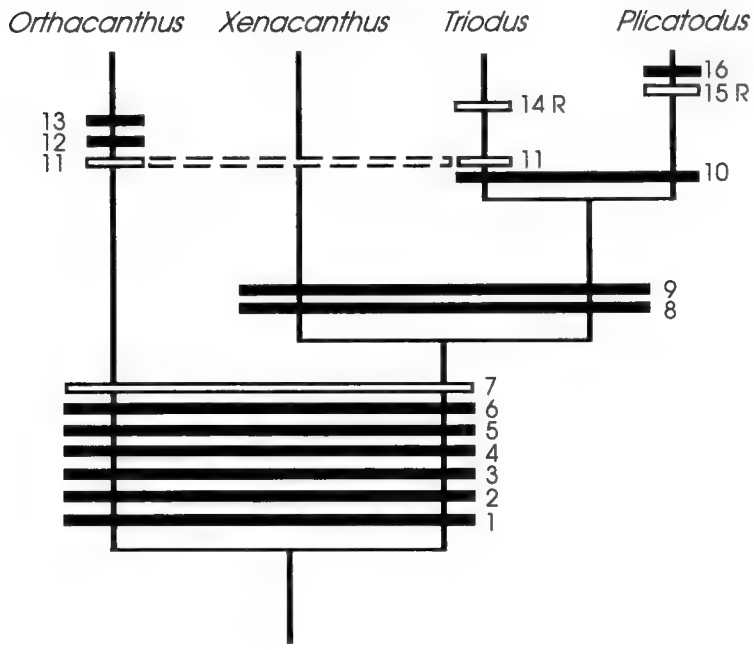


FIG. 7. — Cladogram of the genera of the order Xenacanthida. For explanation, see text. Apomorphous state first, plesiomorphous state second.

Cladogramme des genres de l'ordre des Xenacanthida. Pour les explications, voir le texte. État dérivé en premier, état plésiomorphe en second.

[1] Teeth tricuspidate with distinctly separated cusps; plesiomorphous: teeth often multicuspidate and proximally fused cusps, e.g. in ctenacanthoid sharks;

[2] lack of nutrient foramina on the labial side of the base; plesiomorphous: several nutrient foramina exist on the labial side, e.g. in ctenacanthids;

[3] upperside of base with well defined, strong coronal button: plesiomorphous: lack of a well developed coronal button in ctenacanthids;

[4] bottom side of base with prominent labial process, called basal tubercle; plesiomorphous: no basal tubercle in ctenacanthids, here sometimes only a labial edge, half-moon shaped;

[5] crown consists of orthodentine; plesiomorphous: crown consists of trabecular dentine, all ctenacanthoids;

[6] absence of an enameloid layer; plesiomorphous: crown with enameloid, e.g. in all ctenacanthids;

[7] surface of cusps without sculpture, reversal in [14] and [15]; plesiomorphous: cusps having cristae, generally in ctenacanthids;

[8] dorsal spine with laterally arranged denticles; plesiomorphous: two rows of denticles on the back side of the spine, e.g. in ctenacanthids;

[9] basal tubercle usually with concave depression = apomorphy I for development of the basal tubercle; plesiomorphous: no basal tubercle in ctenacanthids, only half-moon shaped labial edge;

[10] base consists of orthodentine; plesiomorphous: base consists of trabecular dentine, all ctenacanthoids;

[11] number of nutrient foramina regularly less than eight per side of base; plesiomorphous: number of nutrient foramina more than eight, ctenacanthoid sharks;

[12] basal tubercle prominent and rounded = apomorphy II for development of the basal tubercle; plesiomorphous: no basal tubercle in ctenacanthids;

[13] crown with laterally serrated edges; plesiomorphous: no serration known in teeth of ctenacanthoid sharks;

[14] reversal: cusps have straight vertical cristae: parallelapomorphy with ctenacanthids;

[15] reversal: cusps have wavy cristae (hybodont pattern); plesiomorphous: straight vertical cristae, e.g. in a large number of ctenacanthids;

[16] coronal button consists of orthodentine; plesiomorphous: knob-like extremity in ctenacanthids of trabecular dentine.

The Xenacanthida seem to be a monophyletic group, as shown in six synapomorphous characteristics common to all genera.

1. Tricuspidate teeth with distinctly separate cusps.

2. Loss of nutrient foramina on the labial side of the base.

3. Well-defined coronal button.

4. Bottom side of base with clearly separated basal tubercle.

5. Crown made of orthodentine.

6. Absence of a covering enameloid layer.

Generally, the teeth of xenacanthids have lost the sculpture on the cusps in comparison with the ctenacanthids [7]. But some of the genera, as a reversal, redeveloped special types of sculpture again: *Triodus*' cusps have straight vertical cristae [14]. And *Plicatodus* shows a hybodont pattern of wavy cristae [15].

The family Xenacanthidae (including genera *Xenacanthus*, *Triodus* and newly described *Plicatodus*) is distinguished by the following synapomorphies: dorsal spine with laterally arranged denticles [8] and a basal tubercle on teeth, having a usually developed concave depression [9 = apomorphy I for development of the basal tubercle].

Triodus and *Plicatodus* are combined under the synapomorphous character of a base which always consists histologically of orthodentine [10].

Furthermore, *Plicatodus* can be separated by a coronal button which consists of orthodentine, too [16], assessed here as an autapomorphous feature. Other autapomorphous characteristics are present in *Orthacanthus* (only genus within the family Orthacanthidae): distinct and rounded basal tubercle [12 = apomorphy II for development of the basal tubercle] and cusps with laterally placed serrated edges [13].

One homoplasy can be stated, in a number of nutrient foramina regulary less than 8 per side of the base [11], between *Orthacanthus* and *Triodus*.

The geology of the horizon *Plicatodus jordani* came from, the Humberg-Bank, indicates that this xenacanthid probably lived in near-shore environment of large and relatively deep lakes.

Nothing is known about diet, but in analogy to *Triodus* and *Xenacanthus* with partially similar habitats, *P. jordani* might have been able to devour paleoniscoids, acanthodians, and possibly epibenthic organisms like small crustaceans.

Acknowledgements

I like to thank Dr L. EIßMANN, Leipzig, for the loan of the "Lebach"-nodule. I wish to express my cordial thanks to Dr M. MANOUROVA and Dr J. ZAJÍC, Prague, for their cooperation. They enabled the work on the Bohemian material of the Museums' and Surveys' collections. I am very much indebted to Dr H. MERK, Bingen/Rhein for making some x-ray photographs of the nodule and to Mr K. SCHUCHMANN for the preparation of teeth for the histological investigations. I also would like to thank Pr-Dr J.A. BOY, Mainz, Pr-Dr J. SCHNEIDER, Freiberg/Saxony, and Dr C. SCHWIND, Phetchaburi/Thailand, for discussion and valuable advice. The careful review of Dr R. LUND, New York, and Dr C. POPLIN, Paris, is gratefully acknowledged.

ADDENDUM

The new taxon *Plicatodus jordani* was prepublished by SCHNEIDER & ZAJÍC (1994) attached to HAMPE (1994). The name was known by the authors from a manuscript of this article which was submitted on June 1st 1992! However, the definition of the genus is lacking in SCHNEIDER & ZAJÍC (1994). That fails to conform ICZN Art. 13a (i). Therefore, the generic taxon *Plicatodus* is not available after SCHNEIDER & ZAJÍC [see also ICZN Art. 11h (iii); 13c]. The species name "*jordani*" appeared in SCHNEIDER & ZAJÍC only in a legend of a figure (Fig. 27) which shows only the variation of the sculpture on different teeth. A sufficient description is missing. According to this circumstance, the species must be considered as a *nomen nudum*. Moreover, due to the now presented publication, the taxon is made available by a correct definition and it must take the authorship and date of this publication [after ICZN Art. 50, 21; see also p. 260!].

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Section C, n° 1-4 : 227-234.

Ontogenetic development of the squamation in some Palaeoniscoid fishes

by Dmitry ESIN

(A contribution to IGCP 328-Palaeozoic Microvertebrates)

Abstract. — Analysis of the skeleton and numerous scales of *Amblypterina costata* (Eichwald) and *Acropholis* sp. (Actnopterygii, Palaeoniscodei) from the Upper Permian of the East-European Platform permits to distinguish the stages of development of the squamation during growth. There are three main stages: juvenile, subadult and adult, each being characterized by different degrees of expression of the morphological structures, including the shape of the bony plate, the sculpture, the articulation device and the shape of the tubercles on the ganoin surface. The formation of the squamation in palaeoniscids differs from that in living teleosts by the presence of two centres of the squamation development, in the anterior part of the body and the caudal lobe, and by the longer time of development. Apart from these differences, the ontogenetic development of the squamation in these two groups proceeds in the same way.

Keywords. — Actinopterygii, Palaeoniscoidei, Upper Permian, ontogeny, squamation.

Développement ontogénétique de la squamation chez quelques poissons paléoniscides

Résumé. — L'analyse du squelette et de nombreuses écailles de *Amblypterina costata* (Eichwald) et d'*Acropholis* sp. (Actinopterygii, Palaeoniscoidei) du Permien supérieur de la plateforme est-européenne permet de distinguer entre les différents états du développement de la squamation pendant la croissance. Trois états se différencient : juvénile, subadulte et adulte, chacun étant caractérisé par des degrés différents de l'expression de structures morphologiques, dont : la forme générale des plaques dermiques, l'ornementation et la forme des tubercules à la surface de la ganoine. La formation de la squamation des paléoniscides est différente de celle des téléostéens actuels par la présence de deux centres à partir desquels s'ébauchent la squamation, dans la région antérieure du corps et dans le lobe caudal, et par la durée du développement. Dans ces deux groupes, excepté ces différences, le développement ontogénétique de la squamation se déroule de la même façon.

Mots-clés. — Actinopterygii, Palaeoniscoidei, Permien supérieur, ontogénie, squamation.

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INTRODUCTION

The ontogenesis of palaeoniscids has been very little studied. Only a few researchers (BLOT, 1966; SCHULTZE & BARDACK, 1987) have examined some aspects of this complicated problem. The lack of works concerning this problem can be explained chiefly by the scarcity of the material allowing such studies, the poor understanding of the taxonomy of the group, and perhaps some other minor reasons.

The ontogenetic development of the scales and squamation has been studied until now, although the works on this subject could have provided a number of interesting data as to the position of the superorder Palaeonisci among actinopterygians.

The present paper deals with the ontogenetic development of two palaeoniscid species *Acropholis* sp. Elonichthyiformes and *Amblypterina costata* (Eichwald) Palaeonisciformes. The scales of these species are easily distinguished and show some morphological features which are easily observable in their development from the earliest stages, and can be used as reliable taxonomic characters for species and genera.

In addition to the ontogenetic development of the individual palaeoniscoid scales, that of the entire squamation is of considerable interest. Such studies were made by using the whole bodies of the two species mentioned above.

However, the available material was poorly preserved and did not allow adequate comparisons. Therefore, we used the data from SCHULTZE & BARDACK (1987) on size changes in the scales of *Elonichthys hipsilepis* and "*E.*" *peltigerus* from the Mazon Creek Formation (Illinois, USA).

The development of the palaeoniscid squamation during growth was compared with that of the Recent Teleostei (*Carassius auratus*), because the latter have the least number of common features with palaeoniscids, but retain a close relationships with them. The common features of the ontogenetic development of the palaeoniscid and teleost squamations seems thus to be general for the all actinopterygians (Cladistians, Chondrosteans, Holosteans).

MATERIAL AND METHODS

This work on the author's material. collected in the Tikhie Gory Site (Middle Prikamie) and ichthyoliths from the Tongue-4 site (South Priouralie), provided by M. F. IVACHNENKO. The entire bodies and isolated scales of *Acropholis* sp. and *Amblypterina costata* (Eichwald) studied here represent the different growth stages. These two species were selected because of their numerous features which permit the distinction of their scales at all stages in each ichthyolith assemblage from the respective sites. The study of each particular stage was based on the scales from different parts of the body. The recognition of the stage of the scale development was based on the comparison with the body scales in complete individuals of different groth stages. This work incorporates information from the analysis of more than 500 isolated scales of each species, seven skeletons and associated fragments of *Acropholis* sp., and five skeletons of *A. costata*. Detail study was made with CamScan and Jeol scanning electron miscroscopes.

RESULTS

PALAONISCOID SCALE DEVELOPMENT DURING GROWTH

The development of the palaeoniscoid scales proceeds gradually and it is rather difficult to distinguish phases in this process. Nevertheless, we can already recognize three main stages

of the development and three corresponding types of scale structure: juvenile, subadult and adult. There are also intermediate types between there three stages.

Juvenile type

The size of these scales ranges from 0.3 to 0.5 mm. They consist of a quadrangular or rounded bony plate. The presence of the ganoin ridges and their size depend on their position on the body. There are more ganoid ridges on the scales in the centre of the developing squamation than on the margins. In the early stages, palaeoniscoid scales are all similar in structure and can hardly be distinguished. However, the scales of *A. costata* and *Acropholis* sp. in our samples show certain differences. These genera are referred to different orders and their phyletic lineages have diverged rather early, therefore their respective characters occur already in the early stages of their ontogeny.

The majority of the scales in the Palaeonisciformes is characterized by a weak development of the external ornamentation at any stage of their ontogenesis. Even juvenile scales, usually better ornamented than adult ones, possess (in *A. costata)* the flattened ridges, widening at the base. The Elonichthyiformes, and particularly the Acropholiidae, are ornamented with large ridges. The juvenile scales of *Acropholis* sp. usually possess one or two thin ridges, strongly raised above the bony plate. Juvenile scales lack the keel, peg and socket. The characteristic structures of the adult *Acropholis* (e.g. the strongly developed anterodorsal angle of the scale) is not pronounced. The ganoin surface shows a microsculpture which consists of tubercles ranging from 3 to 5 microns (Fig. 1G, H). The tubercles are distributed regularly and cover all the externally exposed ganoin surface. The juvenile scales are characterized by the elongate shape of the tubercles (Fig. 1H). The long axis of the tubercles is directed anteroposteriorly and reflects the main direction of the scale growth.

Subadult type

When at the subadult stage of the development, the scales usually show the basic structure of those of adult individuals (Fig. 1C, D). However, some juvenile features are still present (weak development of the peg and socket articulation, elongate shape of the tubercles in some parts of the squamation). On the external surface of many subadult scales, there are still boundaries between the juvenile ganoin ridges, although the latter tend to fuse and form a uniform ganoin surface. This is best seen in *A. costata* (Fig. 1D).

The tubercles on the ganoin surface are rounded in shape, although they cannot be observed on all scales because the rate of scale growth varies in the different parts of the body. As a result, the tubercles on the scales in the areas of more intensive growth retain an elongated shape. The features which are lacking in juvenile scales (keel, peg and socket) appear at this stage. Some unique characters (e.g. the development of the anterodorsal angle of the scales in *Acropholis* sp.) also appear at this stage.

Adult type

Adult scales have the full set of features : the structure of all scales at this stage are well developed. The scale size in adult *Acropholis* sp. reaches 5-8 mm (Fig. 1E), and 3-5 mm in

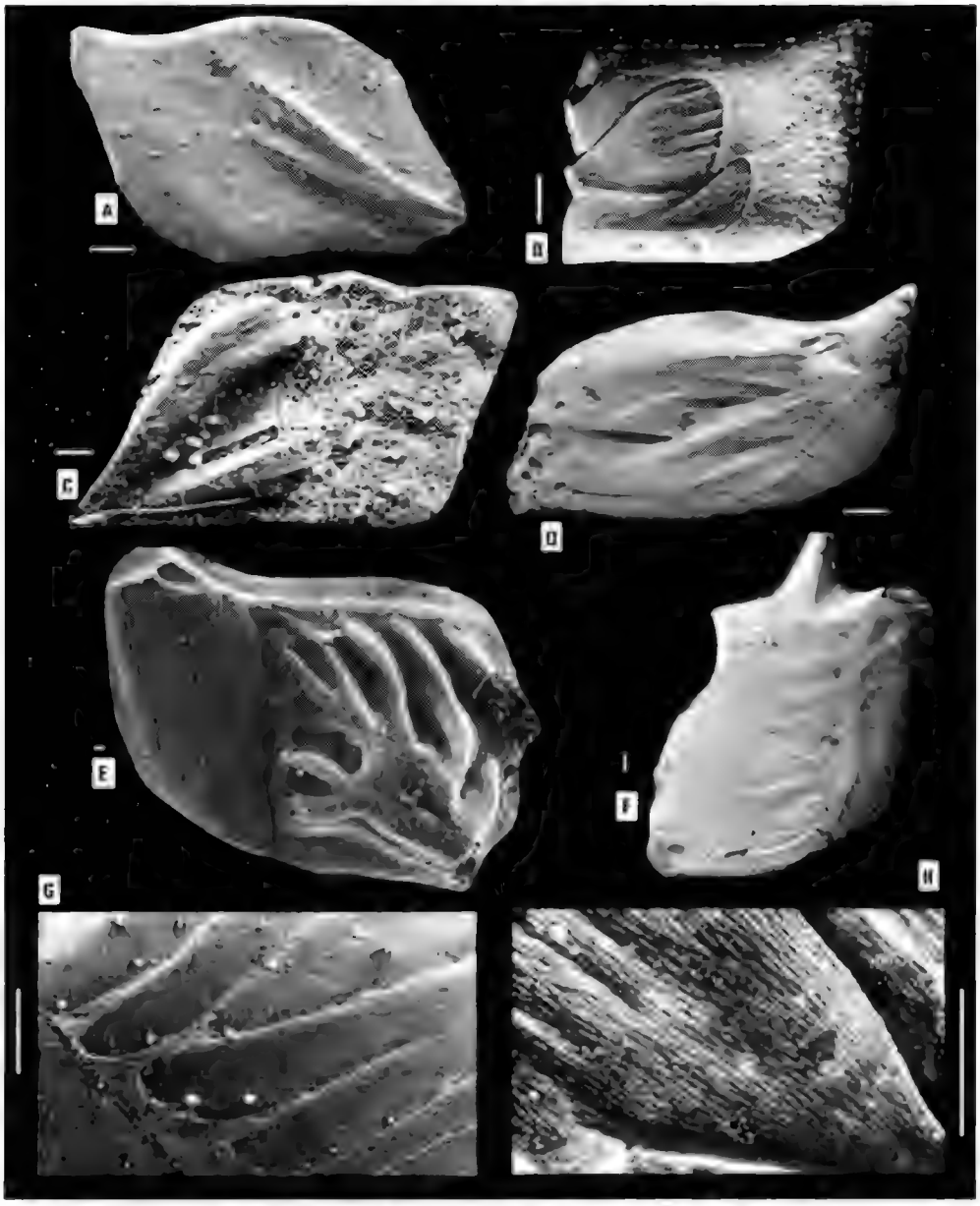

FIG. 1. — Palaeoniscid scales on different stages of the ontogenetic development. A, juvenile scale of *Acropholis* sp. B, juvenile scale of *Amblypterina costata*. C, subadult scale of *Acropholis* sp. D, Subadult scale of *A. costata*. E, adult scale of *Acropholis* sp. F, adult scale of *A. costata*. G, ganoin surface (adult scale). H, ganoin surface (juvenile scale). Scale bar: A-F, 10 µm. G-H, 100 µm.

Écailles de palaeoniscidés à différents stades de leur développement ontogénétique. A, écaille juvénile de Acropholis *sp. B, écaille juvénile de* Amblypterina costata. *C, écaille d'un subadulte de* Acropholis *sp. D, écaille d'un subadulte de* A. costata. *E, écaille adulte de* Acropholis *sp. F, écaille adulte de* A. costata. *G, surface de ganoïne (écaille adulte). H, surface de ganoïne (écaille juvénile). Échelles : A-F, 10 µm ; G-H, 100 µm.*

Amblypterina. The scale acquires taxonomically important features after the completion of the full development of the major morphological elements. Among these features in the *Amblypterina* are the nearly smooth ganoin surface and the characteristic serration of its anterior margin (Fig. 1F). Representatives of *Acropholis* sp. are distinguished by the shape and arrangement of the ridges and the contour of their cross-section.

TRENDS AND TIMING IN SCALE GROWTH

The major changes in the palaeoniscoid scale growth relate to the complexity of the shape and contour of the bony plate and external ornamentation.

The bony plate: in the juvenile stage, the bony plate of the species studied here has a rather simple, rounded or quadrangular outline.

The articular elements are absent and appear only at the subadult stage.

The external ornamentation: the development of the ganoin is more complicated. In the juvenile stage, the external ornamentation of the scales in all palaeoniscids shows one or three ganoin ridges. The latter can be either separated (*Acropholis* sp.) or closely set anteriorly (*A. costata*). The ridges are flattened and quadrangular in cross section. The microsculpture of the ganoin surface consists of elongated tubercles. The subsequent development of the sculpture on the external surface varies. In scales of *Acropholis* sp., the ridges grow faster in height than in breadth. By contrast, in *A. costata*, the ganoin ridges grow laterally, but very little in height. At the subadult stage, the shape of the tubercles on the ganoin surface changes from elongated to rounded. In *A. costata*, the ganoin covers the entire external surface of the scale and the limits between the juvenile ridges are well pronounced. At the same stage of the development, *Acropholis* sp. distinctly shows the bifurcation of the anterior ends of the ridges and the fusion of their caudal ends. The adult stage is characterized by the smoothening of the sculpture. In *A. costata*. the limits between the ridges disappear completely. In *Acropholis* sp., at the same stage, the increasing breadth of the ridges results in their fusion and the subsequent reduction of the sculptured surface. The formation of the anterior margin of the external surface and the sculpture characters are achieved.

SQUAMATION DEVELOPMENT IN THE RECENT TELEOSTEI

The ontogenetic development of the squamation of the living Teleostei is considered on the basis of *Carassius auratus* (DIMITRIEVA, 1957). The formation of the first scales begins when the body length reaches 12-16 mm. The first scales appear on the areas A and B (Fig. 2) and along the lateral line, up to the beginning of the caudal fin. The dorsal and ventral parts remain naked. At the next stage, when the body length reaches 16-19 mm, the scales cover the entire body, except the region between the operculum and pectoral fins. The formation of the squamation is completed when the body length reaches 23 mm. However, it must be noted that this development does not proceed similarly in all Recent teleost. *Rutilus rutilus caspiens*, when less than 18 mm in length, shows the part of the body below the lateral line covered with scales.

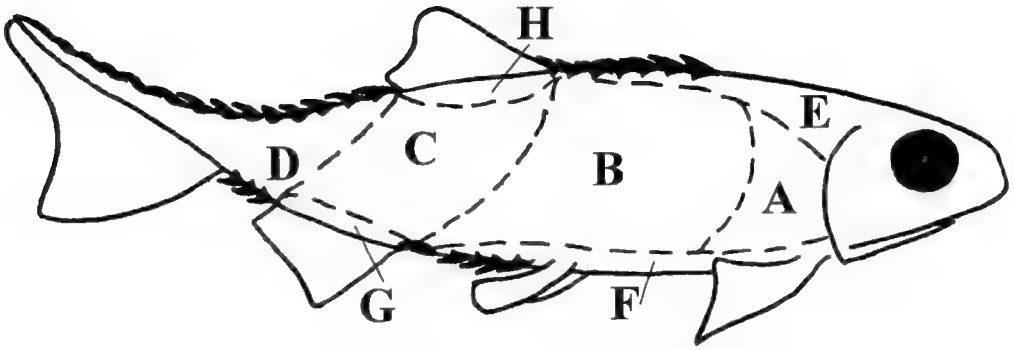

FIG. 2. — The different areas of the squamation in fishes.
Les différentes zones de la squamation chez les poissons.

Lucioperca lucioperca, at the length of 33 mm, has the anterior dorsal and ventral parts free of squamation.

The development of the palaeoniscoid squamation differ from that of the Recent teleosteans, although both share some common features. As SCHULTZE & BARDACK (1987) showed on the basis of the development of the two palaeoniscoid species "*Elonichthys*" *peltygerus* and "*Elonichthys*" *hypsilepis* from the Mazon Creek fauna, and according to my own observations, the formation of the squamation begins in 19-20 mm long individuals. The ridge scales appear first, then the scales of the area "A" (Fig. 2) (ESIN, 1990) and the scales pierced by the pores of the lateral line canal. There are two areas of development of the squamation in the next stage (25 mm). The first one concerns the areas "A", "B", and "C" (partly), and the second one is situated in the caudal lobe. Then, at the length of 34-37 mm, the scales on the areas "C" and "D" meet to form a distinct limit between the body and caudal fin, which show respectively different scale arrangements. The areas around the dorsal, anal, pelvic and pectoral fins remain naked. Later, in the majority of adult palaeoniscids, these regions become covered with small, rounded or quadrangular scales, which have some specific structures.

The squamation samples of *A. costata* and *Acropholis* sp. do not contradict the pattern of squamation development considered above.

DISCUSSION

TAXONOMIC FEATURES

Taxonomically important characters in palaeoniscid ontogeny appear successively. The characters on higher taxonomic rank (order or family) appear by the end of the juvenile stage and are completely formed at the subadult stage. The first of all these features concern the shape of the bony plate and the characteristics of the articulation elements, *i.e.* the shape of the anterior,

upper and lower margins, the length/height ratio, the breadth of the dipping surface, and the shape and size of the peg, socket and keel.

Species-level characters are formed during the transition to the subadult stage of scale development. They usually are represented by ornamentation features of the external surface, *i.e.* the aspect of the anterior margin serration and the shape and arrangement of the ridges, grooves and other structures of the external surface. In the latter phases of the subadult stage, scales undergo some additional alterations but the taxonomically important features remain unchanged.

Palaeoniscoid scales which are in the earliest stage of the development resemble very much those of the earliest actinopterygians (*Andreolepis* and *Lophosteus*) by the lack, or very weak development of the keel, peg and socket, and the ornamentation of the ganoin, represented by elongate, separate ridges.

The absence of the articulation device has at least two explanations. It may be due either to the biogenetic law, or to the active mode of life and intensive body growth in the juvenile stages.

RESEMBLANCES AND DIFFERENCES IN SQUAMATION DEVELOPMENT

Both similarities and differences in the squamation development can be observed between palaeoniscids and teleosteans. Both groups are characterized by the beginning of the squamation development on the flanks of the anterior part of the body and along the lateral line. In both cases, the late stages of the formation of the squamation are marked by the appearance of the scales on the ventral part and around the fins.

The most significant difference is the presence of two independant centres of scale formation in palaeoniscids: on the body and on the caudal lobe. This is not observed in teleosteans.

It is rather difficult to explain the presence of these two zones of squamation development in palaeoniscids. It can be suggested that the development of scales on the caudal lobe may be related to the strong loading on this part of the body when the fish moves. The absence of ossified skeleton, in this case, was presumably compensated by the early appearance of the exoskeleton. Teleosteans avoid such a problem because their endoskeleton is well ossified in the early growth stages.

It is worthy noticing that the first scales to appear in both the palaeoniscids and teleosteans occur at nearly the same stage of the development (viz. at the 14 to 30 mm body length stage), but the squamation in teleosteans' forms is considerably faster. The formation of the squamation in *Carassius auratus* is achieved when the body length reaches 9 mm, whereas in palaeoniscids the ontogenetic changes of the squamation are not achieved at the 60 mm stage, that is, this process takes much more time.

The longer squamation development in palaeoniscids, unlike that of teleosteans, seems to allow the formation of better developed and more complicated structures. The presence of a considerable amount of features in the palaeoniscoid scales strongly increases their taxonomic importance.

Clearly, more knowledge regarding the ontogeny of these fishes is required to resolve this problem.

The study of the development of the squamation and isolated scales may indicate whether the specimen studied should be assigned to a new species or represents another stage of the ontogenetic development of a previously known species.

The shape of the tubercles of ganoin is a useful feature for the determination of the individual stages of the development.

The elongation of the tubercles seems to be the result of the intensive scale growth in the early stages of the development, with a more rapid growth in height than in breadth. In the adult stages, the tubercles are rounded in shape.

The presence of elongated tubercles covering the entire external surface is an evidence for a juvenile stage.

The absence of the squamation in some parts of the body may be evident for the uncompleted individual development. In this case, it should be proved that the specimen under consideration does not represent the juvenile stage of a previously described species. Perhaps, the illustration of the genera *Phanerosteon* (TRAQUAIR, 1877-1914; FRITSCH, 1859), *Kichkassia*, *Lapkozubia* (MINICH & MINICH, 1990), and *Carboveles* are based on such juvenile forms.

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Diabolepis and its bearing on the relationships between porolepiforms and dipnoans

by CHANG Mee-Mann

Abstract. — This study reveals new morphological features of *Diabolepis* based on new specimens and further preparation of previously available materials. Cranial characters are summarized and analyzed in order to provide a basis for discussing the relationships of *Diabolepis*. The cranium of *Diabolepis* shows a number of primitive sarcopterygian characters. Previous hesitation in placing *Diabolepis* in the Dipnoi mainly arose from these primitive sarcopterygian features. In *Diabolepis*, the pterygoid plate and lower jaw bear more dipnoan characters than the cranium. Although these features in the pterygoid plate and lower jaw are typical of the dipnoan condition, uncertainty as to whether the lower jaw, pterygoids and cranium belong to the same animal was used as the main reason for not accepting *Diabolepis* as a dipnoan. The present study reveals further evidence that the lower jaw, pterygoids and the cranium belong to the same form. For example, the processes along the median margin of the dorsal surface of the palatoquadrate fit well into the corresponding fossae on the ventral side of the neurocranium. This is corroborated by similar disposition of dermal bones, tooth morphology and wear patterns shown on the palate and lingual face of the lower jaw. These and other uniquely shared features lend further support to a close relationship between *Diabolepis* and dipnoans. The significance of the *Diabolepis* and its bearing on the close relationship between dipnoans and porolepiforms (including *Powichthys* and *Youngolepis*) are further discussed.

Keywords. — Vertebrata, Sarcopterygii, Dipnoi, Devonian, China, anatomy, phylogeny.

Diabolepis et sa signification quant aux relations de parenté entre les Porolépiformes et les Dipneustes

Résumé. — Cette étude révèle de nouveaux caractères morphologiques de *Diabolepis*, sur la base de nouveaux spécimens et la préparation d'ancien matériel. Les caractères crâniens sont énumérés et analysés de manière à fournir une base à la discussion des relations de parenté de *Diabolepis*. Le crâne de *Diabolepis* présente nombre de caractères primitifs de Sarcoptérygiens, qui sont à l'origine de l'hésitation à placer *Diabolepis* parmi les Dipneustes. Chez *Diabolepis*, les plaques ptérygoïdiennes et la mandibule présentent plus de caractères de Dipneustes que le crâne. Bien que ces caractères des plaques ptérygoïdiennes et de la mandibule soient typiques des Dipneustes, l'incertitude sur leur appartenance au même animal était la principale raison pour ne pas reconnaître *Diabolepis* comme un Dipneuste. Cette étude confirme que le crâne, les mandibules et les ptérygoïdes appartiennent à la même forme. Par exemple, les processus du bord mésial de la face dorsale du palatocarré correspondent bien aux fosses de la face ventrale de l'endocrâne. Cela est corroboré par une disposition similaire des os dermiques, la morphologie dentaire et les surfaces d'usure sur le palais et la face linguale de la mandibule. Ces caractères, ainsi que d'autres, qui sont uniques aux Dipneustes renforcent l'hypothèse d'une relation étroite entre *Diabolepis* et ce groupe. La signification de *Diabolepis* et sa portée quant à la relation entre les Dipneustes et les Porolépiformes (incluant *Powichthys* et *Youngolepis*) sont discutées.

Mots-clés. — Vertebrata, Sarcopterygii, Dipnoi, Dévonien, Chine, anatomie, phylogénie.

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INTRODUCTION

Diabolepis was suggested as the sister-group of all previously known dipnoans when it was described (CHANG & YU, 1984). Since then the problem of its relationship has been discussed by a series of authors, of which some agree with CHANG & YU (MAISEY, 1986; JANVIER, 1986; FOREY, 1987; SMITH & CHANG, 1990) while others variously disagree (SCHULTZE, 1987; SCHULTZE & CAMPBELL, 1987; CAMPBELL & BARWICK, 1987; PANCHEN & SMITHSON, 1987). When *Diabolepis speratus* was first described, the material referred to the species, *i.e.* parts of crania, pterygoids and lower jaw rami, were not found articulated but detached. The cranium shows quite a few primitive sarcopterygian characters, whereas the pterygoid plates and lower jaws look more dipnoan-like. It is precisely the primitive sarcopterygian characters of the cranium that caused hesitation in placing *Diabolepis* among dipnoans (SCHULTZE, 1987: 40). There has been little doubt in referring the pterygoids and lower jaws to dipnoans. The main reason for the pterygoid plates and lower jaws to be assigned to the same species as the crania was the tooth morphology and wear patterns, which are similar to those of the premaxilla, vomer and parasphenoid. In order to find more evidence for suggesting that the cranium, pterygoid plate and lower jaw belong to the same form and to provide the basis for further discussion of the relationships of *Diabolepis* and the interrelationships of sarcopterygians, we present here a survey of the neurocranium and palatoquadrate, together with a summary of the features of the parts of the skull mentioned elsewhere.

ABBREVIATIONS

ano	anterior nasal opening, *narine antérieure*;
asp	ascending process of parasphenoid, *processus ascendant du parasphénoïde*;
c.ju	jugular canal, *canal jugulaire*;
dbpt	dermal basipterygoid process, *processus du basiptérygoïde dermique*;
De	dentary, *dentaire*;
Dmpt	dermometapterygoid, *dermométaptérygoïde*;
dpd	expanded distal portion of dentary, *portion élargie du dentaire*;
Dpl	dermopalatine, *dermopalatin*;
dpp	dorsal palatal process, *processus palatin dorsal*;
d.Pq	depression on visceral side of pterygoid plate occupied by palatoquadrate, dépression sur *la face viscérale de la plaque ptérygoïdienne, occupée par le palatocarré*;
dt	dorsal thikening of pterygoid plate (area of pterygoid plate exposed lateral to palatoquadrate), *épaississement dorsal de la plaque ptérygoïdienne, (région de la plaque ptérygoïdienne exposée latéralement au palatocarré)*;
Ecpt	ectopterygoid, *ectoptérygoïde*;
Enpt	entopterygoid, *entoptérygoïde*;
f.lab	fenestra in wall of otic capsule, *fenêtres dans la paroi de la capsule otique*;.
gr.ju	jugular groove, *sillon jugulaire*;
gr.v.subhy	groove for subhyoidean vein, *sillon pour la veine subhyoïdienne*;

hyd	dorsal articular area for hyomandibular, *surface articulaire dorsale pour l'hyomandibulaire*;
Id1-4	infradentaries 1-4, *infradentaires 1-4*;
la.com	commissural lamina, *lame commissurale*;
lc	lateral commissure, *commissure latérale*;
lp	labial pit, *dépression latérale*;
n. pno	notch for posterior nasal opening, *échancrure pour la narine postérieure*;
om	orbital margin, *bord orbitaire*;
plf	prolingual field, *champ prolingual*;
Pmx	premaxilla, *prémaxillaire*;
Pq	palatoquadrate, *palatocarré*;
Pq.aup	pars autopalatina, *partie autopalatine*;
Pq.pqu	pars pterygoquadrata, *partie ptérygoquadratique*;
Pq.qu	pars quadrata, *partie quadratique*;
ptp	pterygoid tooth plate, *plaque dentaire ptérygoïdienne*;
r.supj	suprajugular ridge, *crête suprajugulaire*;
s.soc	bone series carrying supraorbital sensory canal (nasal series), *série d'os portant le canal de la ligne sensorielle supra-orbitaire (série nasale)*;
s.st	supratemporal series, *série supratemporale*;
W-l	Westoll-lines, *lignes de Westoll*.

DESCRIPTION

Skull roof and sensory line canals

The following account is largely based on specimens V7237 (Fig. 1) and V7238 where the skull roof is complete. Reference is made to V7241 (with only the snout preserved) where necessary. The former two specimens differ in shape and proportion. In V7237 the skull roof is broader and its maximum breadth (measured at the level of the posterior margin of the orbit) is 83% of the total skull length, while in V7238 it is 67%. In V7238 the orbit is much larger (its diameter is 25% of the skull length) than in V7237 (15%), hence more posteriorly situated posterior margin of the orbit (Fig. 2). This makes the portion of the skull roof anterior to the posterior margin of the orbit and the prepineal length in V7238 (45% and 39% of the skull length) much longer than those of V7237 (37% and 33% respectively). As noted by Chang & Yu (1984), the smaller size of V7238 (only half the length of V7237) suggests that it is most probably a juvenile individual and this is consistent with the observation that the orbit is comparatively larger in juvenile fishes than in adults (cf. Schultze, 1984: 5).

Despite of the differences in proportion and shape, the two specimens show a similar bone pattern in the skull roof. The dorsal surface is on the whole plane. No pineal opening has been observed, though a distinct median elevation at the level of the posterior part of the orbit marks the position of the pineal body. In V7237, the skull roof is slightly domed anterior to the pineal elevation, between the supraorbital sensory canal loops, whereas in V7238 and V7239 a distinct

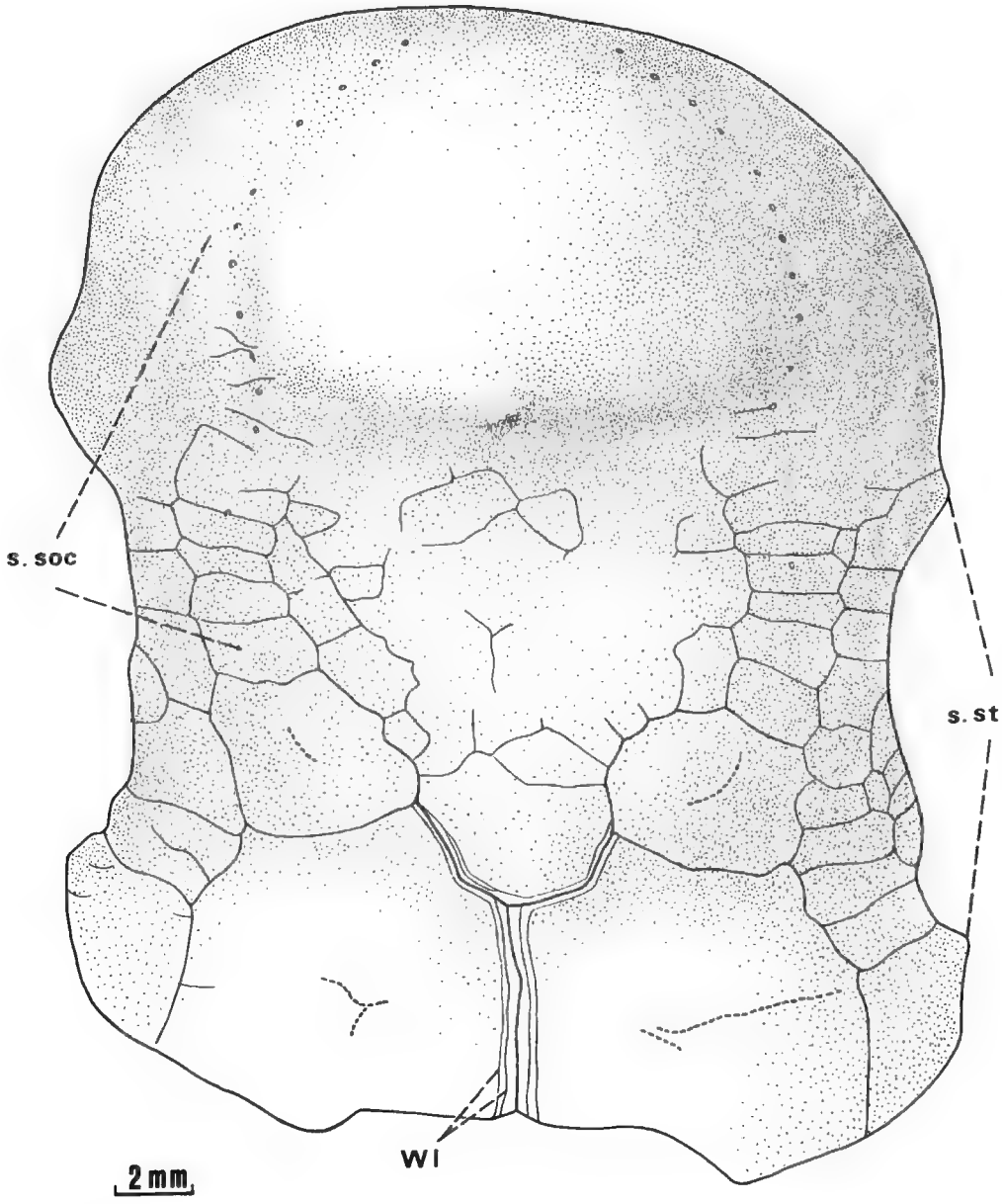

FIG. 1. — *Diabolepis speratus* (CHANG & YU), Lower Devonian, Yunnan, China. Skull roof in dorsal view, (from CHANG & YU, 1984, Fig. 1B).

Diabolepis speratus *(CHANG & YU), Dévonien inférieur, Yunnan, Chine. Toit crânien en vue dorsale, (d'après CHANG & YU, 1984, fig. 1B).*

small depression is present behind the pineal elevation. No suture can be seen in the anterior part of the skull roof, except for one that bounding the premaxilla.

The skull roof is not divided into anterior and posterior shields, as it is in non-dipnoan sarcopterygians. CHANG & YU (1984) suggested that the pair of bones at the rear of the skull roof, that bear the middle and posterior pit-lines can be compared with the I-bones of dipnoans, or postparietals (parietals of CHANG & YU) in other sarcopterygians. The pair of bones in front of I-bones, bearing the anterior pit-lines, was in turn compared with the J-bones of dipnoans, or parietals (frontals of CHANG & YU) of other sarcopterygians. If the posterior border of the J-bone is taken as the boundary between the anterior and posterior portions of the skull roof, comparable to the fronto-ethmoidal and parietal shields (according to JARVIK's terminology) of non-dipnoan sarcopterygians, then the anterior portion is rather long, representing 73% of the skull length in V7237 and 80% in V7238. The J-bones and the anterior portions of the I-bones are separated by a median element, suggested to be the B-bone. Along the posterior margin of the B-bone and the anteromedial and medial margins of the I-bones, fine but distinct, concentric

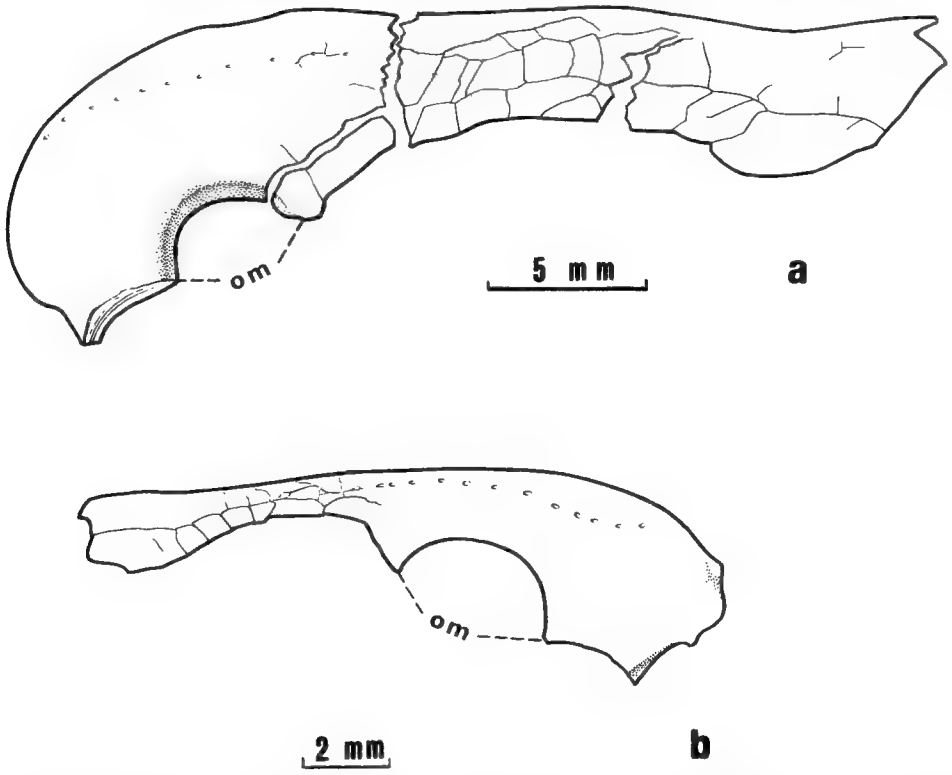

FIG. 2. — *Diabolepis speratus* (CHANG & YU), Lower Devonian, Yunnan, China. Skull roof in lateral view. A, specimen V7237; B, specimen V7238.

Diabolepis speratus *(CHANG & YU), Dévonien inférieur, Yunnan, Chine. Toit crânien en vue latérale. A, spécimen V7237 ; B, spécimen V7238.*

lines have been observed. No doubt they are Westoll-lines. In V7237 the B-bone is anteriorly delimited by faint sutures. These, and other complete and incomplete sutures in front of them, mark out a mosaic of small bones, which are variable in size and shape. In V7238 there are no sutures to indicate the anterior margin of the B-bone, which thus merges imperceptibly into the anterior portion of the skull roof. The bone series carrying the supraorbital sensory canal and sutures marking a few small bones medial to the posterior ones of this bone series are seen in both V7237 and V7238. The bone series traversed by the supraorbital sensory canal, apparently comparable to the nasal series, or K, L, etc. bone series as suggested by CHANG & YU, extends backwards well beyond the orbit. The posterior elements of this series, are delimited by distinct sutures and are short and broad, transversely elongated, with parallel anterior and posterior borders, and are roughly hexagonal in shape. Lateral to this bone series, behind the orbit, the lateral margin of the skull roof is formed by another series of small bones, which are often pentagonal in shape. We suggest that they correspond to the supratemporal series (X, Y1, Y2-bones). The series is long in both specimens, approximately 60% of the total skull length in V7237 and 45% in V7238. The pentagonal and hexagonal series of bones are tightly interlocked. In V7237, lateral to the marginal series, at the level of the J-bone, there are several bones of still smaller size and irregular shape. The number of bones in all these series varies from specimen to specimen and from one side to the other in the same specimen.

The premaxilla is the only separate bone in the snout. No sensory canal pore has been observed to pierce the bone. It consists of a broad anteromedial and a narrow posterolateral divisions. Owing to the marked downward and inward bending of the mouth a considerable portion of the anteromedial division and the entire posterolateral division lie inside the mouth cavity. The proportion of the premaxilla which remains outside the mouth cavity and is covered with cosmine varies from specimen to specimen. In V7239 and V7240 the portion remaining outside is relatively large, with distinct sutures between it and the adjacent bones, whereas in V7237 it is much smaller and seems to be squeezed between the adjacent bones with no smooth sutures (Fig. 3). In V7238 the premaxilla is not preserved. The anterior external nasal opening is situated ventrally, lying at the margin of the mouth, with the premaxilla as its ventral (posterior) border. Lateral to the anterior nasal opening, the anterolateral margin of the skull roof shows a long and narrow overlap area, apparently for the lacrymal. Medial to this overlap area, the margin shows a rounded notch having a cosmine-covered border. The posterior nasal opening is most probably located in this notch, dorsal (anterior) to the distal portion of the premaxilla. In any case, both nostrils must thus be situated dorsal (anterior) to the premaxilla. The expression "outside (or inside) the mouth cavity" is not used here because it is not topographically accurate. A narrow area of bone, which merges posteriorly with the skull roof, divides the two nasal openings. This area of bone may correspond to the lateral rostral of osteolepiforms and porolepiforms.

The course of the supraorbital sensory canal is shown by single row of pores opening on the skull roof. As mentioned above, the posterior portion of the canal is carried by a series of clearly delineated small bones. As in V7238, the supraorbital sensory canal pores are often situated in the sutures between these small bones. In the same specimen, the posteriormost pores for this canal lie at the suture between the J-bone and the anteriorly adjoining element of the small bone series. This suggests that the posterior end of the supraorbital sensory canal extends backwards into the J-bone and ends anterolateral to the anterior pit-line. There is no postorbital

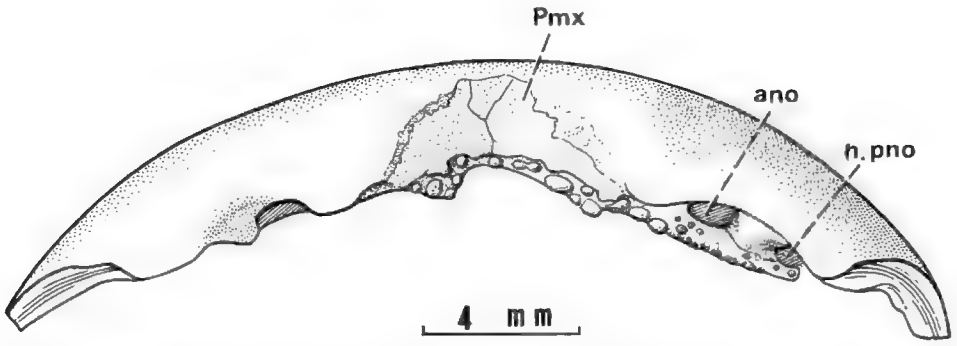

FIG. 3. — *Diabolepis speratus* (CHANG & YU), Lower Devonian, Yunnan, China. Snout in anteroventral view, V7237.
Diabolepis speratus *(CHANG & YU), Dévonien inférieur, Yunnan, Chine. Museau en vue antéroventrale, V7237.*

junction between the supraorbital and infraorbital sensory canals. In the snout, no pores of the infraorbital sensory canal can be seen, but the suture between the premaxilla and the adjoining part of the skull roof behind it exhibits a number of kinks in V7239, V7240 and V9527, it turns upon itself more or less abruptly at several points, like the corresponding suture in *Youngolepis*. In this last form the pores through which branching tubes from the infraorbital sensory canal and the ethmoidal commissural canal open to the surface are situated at the kinks in the suture (CHANG, 1982, Fig. 6C). Pores of this kind seem also to be present at certain kinks in the suture in V7239. The anterior portion of the infraorbital canal and the ethmoidal commissural canal were discovered by serial grinding of *Youngolepis* (CHANG, 1982, Fig. 4, secs. 19, 24), but there is no direct observation so far to confirm the presence of these parts of the canals in *Diabolepis*. In *Youngolepis*, posterior to the premaxilla, the bone probably corresponding to the lateral rostral in *Eusthenopteron* (CHANG, 1982, Figs. 5D, 6C), which forms the ventromedial border of the anterior external nasal opening and sutures with the premaxilla from behind, roofs the sections of the sensory canals mentioned above (CHANG, 1982, Pls 8.5). In *Diabolepis*, where no similar bony strip under the anterior nasal opening exists, these sections of the infraorbital and ethmoidal sensory canals, if present, could only lie in the skin above the lower border of the anterior nasal opening, but not enclosed in bone. Moreover, as noted above, the suture bounding off the premaxilla in V7237 has an entirely different appearance than that in V7239 and V7240. Thus, it is not unwise to assume that the anterior portions of the infraorbital and ethmoidal commissural canals in *Diabolepis* are either absent or interrupted at the anterior nostril. No pore of the main sensory canal can be traced on the dorsal surface of the skull. The restoration of the course of this canal by SCHULTZE & CAMPBELL (1987, Fig. 1d) is obviously made according to convention, not from the specimens.

Under the lateral edge of the posterior elements of the supratemporal series, a laterally facing longitudinal groove, similar to that in *Youngolepis* (CHANG, 1982, Fig. 4 secs. 392-444), is seen in V7237 and V7238. It is conceivable that the main canal, like that in *Youngolepis*, ran along the edge of the supratemporal series.

The anterior pit-line is restricted to the J-bone in both V7237 and V7238. The middle and posterior pit-lines are normal and symmetrical. The middle pit-line extends to Y2 in V7238,

while in V7237 the lines vary in course and extension (Fig. 1). This kind of variation is commonly met with in dipnoans (MILES, 1977).

The extrascapular series is not preserved.

Among osteichthyans, the skull roof pattern of *Diabolepis* comes closest to that of dipnoans on the basis of the following shared characters:

1. there is a median bone (B) in the posterior part of the skull roof;

2. the bones carrying the anterior and middle + posterior pit-lines are separated or partially separated by this median bone;

3. the supraorbital sensory canal extends back to the J-bone, but not to the supratemporal series, and there is no postorbital junction between it and the infraorbital canal;

4. the infraorbital canal is probably interrupted at the anterior nostril;

5. the posterior elements of the nasal series and the anterior elements of the supratemporal series lie side by side;

6. there are Westoll-lines.

Diabolepis agrees with primitive dipnoans (*i.e. Dipnorhynchus* and *Uranolophus*) but differs from later ones in:

1. I-bones meeting behind the median B-bone;

2. supraorbital sensory canal entering J-bone without joining the infraorbital canals posterior to the orbit, in contrast with the supraorbital canal extending from the nasal to supratemporal series and joining the infraorbital canal in X-bone in later dipnoans;

3. parts of the nasal series and supratemporal series lying in the same transverse plane rather than one series lying in front of the other, as in later dipnoans.

In addition, the snout in *Diabolepis* is comparatively short, the orbit and the pineal elevation are relatively anteriorly positioned, and the supratemporal series (X Y1, Y2) is, like in early dipnoans, longer than in later ones. As mentioned above, the length in V7237 and V7238 is 50% and 45% respectively of the skull length, while it is 50% for *Uranolophus* and 44% for *Dipnorhynchus*, but in *Chirodipterus australis* it is between 39% and 46% (MILES, 1977: 232).

Regarding other sarcopterygians, the skull roof of *Diabolepis* shows greater similarity to *Youngolepis* than to other forms. In both genera the premaxilla is a separate bone and not traversed by a sensory line (shared also with *Powichthys* and coelacanths), and the main lateralline canal runs alone the lateral edge of the skull roof. If the J-bone can be homologized with the parietal, so that its posterior margin is the posterior margin of the anterior portion (frontal shield) of the skull roof, then this portion in *Diabolepis*, *Youngolepis* and *Powichthys* is rather long, at any rate longer than that of all other non-dipnoan sarcopterygians.

NEUROCRANIUM AND DERMAL BONES COVERING ITS VENTRAL SURFACE

Ethmoidal region

This region is broad and short in *Diabolepis*. Its ventral face is, in large part, covered by the premaxilla and vomer. In all specimens where the premaxilla is preserved, as a result of the

strong downward bending of the snout, much of its anteromedial division and the entire posterolateral division lie inside the mouth cavity and are entirely covered with blunt teeth that show traces of wear. In V7239, where a large portion of the premaxilla lies inside the mouth, the teeth (or perhaps tubercles) are of rather irregular shape, especially those situated next to the cosmine covering on the exposed portion of the premaxilla. The premaxilla is thin and narrow at its posterior end and the length of this posterior division varies; in some specimens it does not reach the level of the postnasal wall. Posterior to the premaxilla the ventral face of the

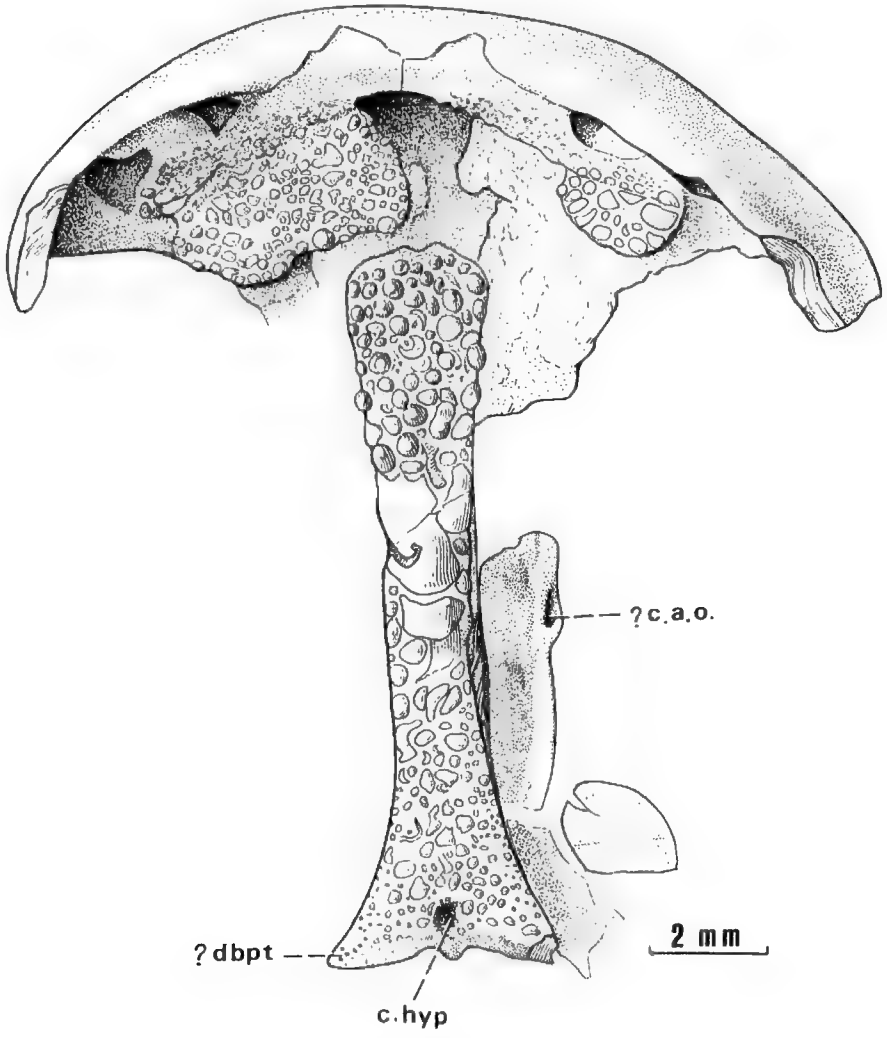

FIG. 4. — *Diabolepis speratus* (CHANG & YU), Lower Devonian, Yunnan, China. Anterior cranial division in ventral view, V9527.
Diabolepis speratus *(CHANG & YU), Dévonien inférieur, Yunnan, Chine. Division crânienne antérieure en vue ventrale, V9527.*

ethmoidal region is covered by a paired vomer of rectangular shape, studded entirely with teeth which merge with the tooth-bearing portion of the premaxilla to form a continuous tooth patch. The bone area between the two nasal openings may also bear teeth or tubercles. Thus on the left side in the newly prepared specimen V9527 (Fig. 4), this area and the medial border of the anterior nasal opening formed by the premaxilla are studded with teeth or tubercles, while in V7237 the medial half of the area is covered by cosmine and the left half with tubercles. In V7240 the area is comparatively extensive and entirely covered with smooth cosmine. This variation in the tooth-bearing portion of the upper jaw indicates that the position of the outer border of the portion of the upper jaw occluding with the tooth-bearing portion of the lower jaw (see below) varies in different specimens. And if we take the outer border of the tooth-bearing portion as the mouth margin, then the position of this margin varies from specimen to specimen.

In specimens where the vomer is not preserved, the vomerine area shows an uneven surface divided by grooves into raised areas of irregular shape and size, and looks exactly like this area in *Youngolepis*. Between the two vomers is the only exposed area of the ventral face of the ethmoidal region. When the vomers are in position, a deep depression is formed in the midline between them and the premaxillae.

The ventral portion of the postnasal wall is rather thick, especially laterally. This wall, unlike the roughly transverse postnasal wall of that of the non-dipnoan sarcopterygians, stretches obliquely posteromedially, and passes gradually into the lateral wall of the orbitotemporal region. The surface of the ventral margin of the postnasal wall is smooth and bears no sign of a lateral

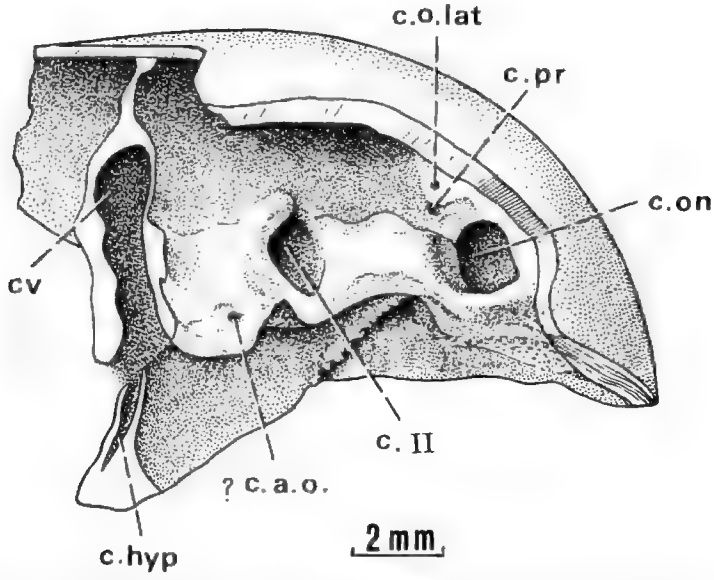

FIG. 5. — *Diabolepis speratus* (CHANG & YU), Lower Devonian, Yunnan, China. Anterior cranial division in postero-ventrolateral view showing the openings in the postnasal and lateral walls of the neurocranium, V7239.

Diabolepis speratus *(CHANG & YU), Dévonien inférieur, Yunnan, Chine. Division crânienne antérieure en vue postéro-ventrolatérale, montrant les ouvertures dans les cloisons postnasale et latérale du neurocrâne, V7239.*

articular area for the palatoquadrate comparable to that in *Eusthenopteron* (JARVIK, 1942, Fig. 48) and porolepiforms (JARVIK, 1972, Pl. 9.2; BJERRING, 1989, Fig. 2A). The same smooth ventral surface of the postnasal wall is also seen in *Youngolepis*, *Powichthys* and dipnoans. Three openings are visible on the posterior face of the postnasal wall (Fig. 5). The largest, situated in the ventromedial part of the wall, can easily be compared with the orbitonasal canal in *Youngolepis* and other sarcopterygians. A small opening situated in the dorsomedial part of the wall, just under the skull roof, was most probably traversed by the ramus ophthalmicus lateralis. The third opening lies between these two, in the medial portion of the postnasal wall, and is comparable with profundus canal in other sarcopterygians.

A network of fine, reticulating canals uncovered through a break in the dorsal wall of the right nasal cavity of V7241 recalls the rostral tubuli in *Youngolepis*, *Powichthys* and dipnoans.

Orbitotemporal region

In this region the braincase is narrow and deep. Extending dorsolaterally, just behind the ethmoidal region and tightly applied to the lower face of the skull roof, is the extensive tectum orbitale (CHANG & SMITH, 1992, Fig. 10). How far it extends backwards can not be made out. The median portion of the ventral face of this region is occupied by the long, narrow parasphenoid which bears a prominent dentition and extends anteriorly to the ethmoidal region where it meets the vomer. The parasphenoid thus prevents the pterygoids from meeting at the midline. The anterior portion of the parasphenoid shows some variation in tooth arrangement. In V7239, there are three longitudinal rows formed by rather large teeth (CHANG & YU, 1984, Fig. 2A, B). In V7240, the median row is formed by three large teeth and the second of them is clearly folded at the base, while the two lateral rows of smaller teeth are not regularly arranged (CHANG & YU, 1984, Fig. 2C, D). All large teeth are worn. In V9527 (Fig. 4), the anterior portion of the parasphenoid is covered with randomly scattered teeth of different sizes and a few new, unworn teeth can be observed in places where old teeth are worn or partially resorbed. The middle portion of the parasphenoid, which is usually the deepest portion of the bone and hence most subject to wear, is, in large part, covered with extensive patches of worn dentine rather than by discrete teeth. Posterior to this part the teeth become smaller and irregular in shape. V7240 and V9527 show the bucco-hypophysial opening in a depression in the posterior part of the parasphenoid. Around the opening are small denticles. The parasphenoid is flanked along its entire length by deep, dorsomedially extending wings, which give it a troughlike dorsal surface. This trough accommodates the high and narrow ventral part (including the suborbital ledge) of the interorbital portion of the braincase. The lateral surface of the parasphenoid wing bears long, irregular grooves and ridges running obliquely anterodorsally. The parasphenoid in V9527 ends abruptly behind the bucco-hypophysial opening and has a tiny medial process along the posterior margin. Immediately posterior to the opening, the posterolateral corners of the parasphenoid protrude to form a pair of pronounced processes. In V7240 the parasphenoid shows a pair of short lateral processes at approximately the same level as in V9257. The parasphenoid in this specimen extends further backwards than in V9527, and posterior to the short process just mentioned there is another pair of fairly high ascending processes, which extend dorsolaterally to abut against the lateral wall of the neurocranium posterior to the basipterygoid process (CHANG & YU, 1984). This posterior pair of processes in V7240 can be compared with the ascending

processes of the parasphenoid in other osteichthyans, though it is absent in coelacanths and dipnoans. If this interpretation is correct, the anterior pair of processes seen in both V7240 and V9527 must be homologous with the dermal basipterygoid process, otherwise present only in advanced actinopterygians (GARDINER, 1984: 276). The parasphenoid is restricted to the anterior cranial division and does not cover the ventral surface of the otoccipital region.

The large optic nerve foramen opens anteriorly in the lateral wall of the braincase where it is surrounded on its upper, posterior and lower margins by a thick ridge (Fig. 5). The ventral wall of the neurocranium is wide anteriorly to the optic foramen, and bears a pair of broad fossae delimited by the vomer anteriorly and the parasphenoid medially. Each of these fossae extend medially between the suborbital ledge (or subocular shelf), which is enclosed in the lateral wings of the parasphenoid and the ventrolateral face of the braincase, dorsolaterally to the parasphenoid (Fig. 11). They correspond topographically to the fossa autopalatina in *Porolepis* (JARVIK, 1972, Figs. 9A, 16A-C, 20A, B; BJERRING, 1989, Fig. 2A) *Powichthys* (JESSEN, 1980, Fig. 5) and *Youngolepis* (CHANG, 1982, Figs. 7A, 15A), but extend much further medially. The dorsolateral margin of each fossa is thickened into a ridge which probably corresponds to the "olfactory ridge" (or crista suspendens) in *Porolepis* (JARVIK, 1942, Fig. 37) and *Powichthys* (JESSEN, 1980, Fig. 5) and the similar structure in *Youngolepis* (CHANG, 1982, Fig. 15A). As a matter of fact, the term "olfactory ridge" was originally proposed by JARVIK (1937: 95; Figs. 10-16) for *Eusthenopteron wenjukowi* to designate a longitudinal, rounded ridge on the lateral face of the anterior portion of the orbitotemporal region. This ridge, which embraces the olfactory canal, extends from the medial part of the postnasal wall backwards almost to the optic foramen. Ventral to the olfactory ridge in *Eusthenopteron wenjukowi*, the lateral face of the orbitotemporal region is provided with a strongly developed, downwardly directed crest, the crista suspendens (JARVIK, 1937, Figs. 10-16). In *Eusthenopteron foordi* the crista is not situated immediately below the olfactory ridge, but is in the form of a few protuberances on the thin, ventral part of the interorbital wall (JARVIK, 1937: 101; 1942: 439; Figs. 47B, 48-50). In *Porolepis* the term "olfactory ridge" was applied to a ridge on the ventrolateral border of the orbitotemporal region, extending from the ventromedial part of the postnasal wall backwards, ventrally to the optic foramen. At the transition between the ethmoidal and orbitotemporal regions in *Porolepis*, the ridge is rather sharp and directed slightly downwards and to this sharp part of the ridge the term "crista suspendens" was applied (JARVIK, 1942: 361; Fig. 37; Pl. 3.1, 2; Pl. 4). In fact, the "olfactory ridge" in *Porolepis* seems to have little to do with the olfactory canal, and the crista suspendens is just a more pronounced part of the ridge. The ridge, together with the crista, forms the upper border of the fossa autopalatina which is unique to porolepiforms, *Powichthys*, *Youngolepis* and *Diabolepis*. In *Powichthys* and *Youngolepis*, the term "olfactory ridge" was borrowed from porolepiforms for the ridge bordering the fossa autopalatina from above. In both forms, the ridge usually extends posteroventrally from the posterior margin of the articular area for the ethmoidal process of the palatoquadrate, and runs ventral to the optic foramen to merge posteriorly with the horizontal portion of the basipterygoid process (JESSEN, 1980, Fig. 5; CHANG, 1982, Fig. 15), and as in *Porolepis* it has nothing to do with the olfactory canal. It is approximately in the position of the "olfactory ridge" (and crista suspendens) in *Porolepis* and the crista

suspendens in *Eusthenopteron wenjukowi*. Therefore, the term crista suspendens is used here instead of olfactory ridge in *Powichthys, Youngolepis, Diabolepis* and porolepiforms.

In different specimens of *Youngolepis* the size and the extent of the fossa autopalatina varies considerably. In most specimens, behind the articular area for the ethmoidal process of the palatoquadrate the ventral wall of the braincase extends laterally well beyond the lateral margin of the parasphenoid (CHANG, 1982, Figs. 4 sec.130, 7A, 10; Pls 8.1, 3-5, 10, 11.1). In some specimens, e.g. V6179, the sharp crista suspendens ("olfactory ridge" in CHANG, 1982, Fig 15) is well-developed, and merges posteriorly with the horizontal portion of the basipterygoid process. In such specimens a rather deep fossa autopalatina is formed between the ventral wall of the braincase and the usually well-developed suborbital ledge. In other specimens where the crista suspendens is less developed and rounded or even hardly noticeable, and not continuous posteriorly with the horizontal portion of the basipterygoid process, the fossa autopalatina is shallow and the suborbital ledge is narrow (e.g. V6227: CHANG, 1982, Pl. 11, 2). In different genera and species of porolepiforms the situation also varies. In *Glyptolepis groenlandica* both the ventral wall of the braincase and the suborbital ledge with the parasphenoid are very broad, the anteromedial articular lamina of the palatoquadrate is deeply inserted in the fossa autopalatina and even fused in one or two areas with the suborbital ledge (JARVIK, 1972: 71; BJERRING, 1989, Fig. 2A), while in a specimen of *Glyptolepis* (BMNH, P. 47838) from the Middle Old Red Sandstone near Pennyland the suborbital ledge is narrow, the crista suspendens is hardly discernible, and the fossa autopalatina is shallow. In *Porolepis* and *Youngolepis*, the ventral wall of the braincase extends laterally beyond the lateral margin of the parasphenoid (JARVIK, 1972, Fig. 9A) and the crista suspendens extends posteriorly dorsal to the horizontal portion of the basipterygoid process (JARVIK, 1972, Fig. 20A). In some specimens of *Porolepis* the fossa autopalatina is deep but in others it is shallow and no articular areas devoid of periosteal lining has been found (JARVIK, 1972: 5455). In *Holoptychius* the fossa autopalatina is deep and the crista suspendens extends backwards to join the horizontal portion of the basipterygoid process (JARVIK, 1972, Fig. 20B). *Powichthys* does not show a well-developed fossa autopalatina (JESSEN, 1980: 199).

In *Diabolepis*, there is an elongated depression on the underside of the anterior part of the crista suspendens (Fig. 11), possibly receiving a similarly shaped process from the palatoquadrate (see below). Further backwards, posterior to the fossa autopalatina and ventrally to the optic foramen, the ventrolateral wall of the neurocranium bears a rather deep and well-delineated depression on either side of the parasphenoid. There is no periosteal lining in the bottom of the depression, and it is probable that it is one of the areas where the palatoquadrate articulates (see below). In as much as no comparable structure has yet been found in closely related form, the depression is named from its topographical position as the suborbital fossa. Behind this depression, posteroventral to the optic foramen, the lateral wall of the orbitotemporal region exhibits a small opening which, in V7239, is surrounded by pronounced ridges and a stout, rounded process on its ventral side. In V7240, however, it is followed by a groove on the ventrolateral surface of the braincase (CHANG & YU, 1984, Fig. 2D). This opening cannot be interpreted at present, but judging from its position and by comparison with primitive dipnoans, it seems probable that it was traversed by the ophthalmic artery. In V7240, there is a well-developed basipterygoid process similar to that of porolepiforms and *Youngolepis*, with laterally expanded

horizontal and dorsal portions, but situated higher on the lateral wall of the braincase. In porolepiforms, *Powichthys* and *Youngolepis* the basipterygoid process is situated low down, and its anterior horizontal portion is either continuous with the crista suspendens (*Glyptolepis, Holoptychius, Powichthys* and most specimens of *Youngolepis*) or at the same level as the suborbital ledge (*Porolepis* and some *Youngolepis*). In osteolepiforms the position of the basipterygoid process is rather high and the suborbital ledge turns up steeply to merge into the basipterygoid process (JARVIK, 1980, Fig. 86A). No descending process of the sphenoid (JESSEN, 1980) has been found in *Diabolepis*.

Otic region

V7237 is the only specimen with a prepared posterior part of the neurocranium. In this specimen the occipital portion, together with the cranial portion of the notochordal canal, is missing. Similar examples are often seen in *Youngolepis* where the occipital region of the neurocranium is separated from the otic region by a lateral occipital fissure which runs downwards from the posterodorsal part of the neurocranium and bends forwards ventrally to reach the posteromedial corner of the vestibular fontanelle. Although the ventral surface of the otic region is badly damaged, the remaining part (Fig. 6A) still show striking similarities to *Youngolepis*. The dorsal surface of this region is tightly applied against the dermal bones of the skull, leaving no space for ridges or muscle insertions. The lateral commissure, as in *Youngolepis*, stretches posterodorsally and forms the lateral wall of the wide jugular canal. Though its posteroventral surface is damaged, one can infer from its similar extension to that of *Youngolepis* that the articulation of the hyomandibula was rather extensive and most probably consisted of two areas. Posteriorly, the jugular canal is followed by the wide jugular groove on the ventrolateral face of the otic region. The dorsolateral margin of the groove is bounded off by a ridge similar to the suprajugular ridge in *Youngolepis* (CHANG, 1982: 52; Fig. 12: = jugular ridge in *Eusthenopteron*, JARVIK, 1980, Fig. 86). This ridge follows the curve of the jugular groove and is interrupted anteriorly by another groove running laterally probably for the subhyoidean vein, as was suggested for *Youngolepis*. The ridge is rather weak and bears no obvious process at its posterior end comparable to the parampullar process in *Youngolepis*. The ventral margin of the ventromedial wall of the jugular groove is broken. On the posterior portion of the preserved part of the wall there is a large notch with periosteal lining. This must represent the upper margin of the large foramen in the lateral wall of the otic capsule which otherwise is present only in *Youngolepis* (CHANG, 1982: 53) and *Nesides* (JARVIK, 1954, Fig. 4A). So far as it has been possible to prepare it, the cranial cavity in the otoccipital region is almost identical with that of *Youngolepis*. Since no wall are preserved between the otic capsules and the cranial cavity, the cranium in this region displays a large cavity. A *Youngolepis* specimen (V6557) in the same state of preservation as to the otoccipital region shows exactly the same structure (Fig. 6b).

PALATE

Dermal palate

The dermal palate in *Diabolepis* is represented by a single pair of tooth plates, the pterygoid plates. The plates have already been described in detail by CHANG & YU (1984) and SMITH &

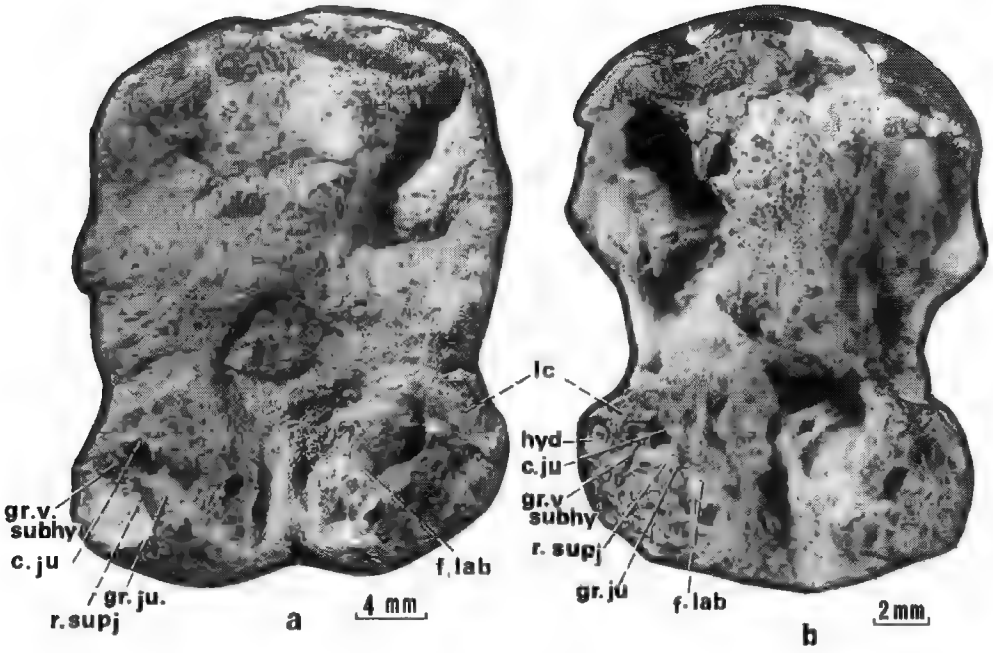

FIG. 6. — Incomplete crania in ventral view showing dorsolateral part of otic region. A, *Diabolepis*, V7237. B, *Youngolepis*, V6557.

Crânes incomplets, en vue ventrale, montrant la partie dorso-latérale de la région otique. A, Diabolepis, *V7237. B,* Youngolepis, *V6557.*

CHANG (1990). Only a summary is presented here for further discussion. The pterygoid plate has a fairly broad horizontal portion and a comparatively small postero-ventrolaterally curved quadrate ramus. The buccal surface of the horizontal portion is slightly concave and bears regular rows of teeth while the medial, posteromedial, and lateral margins of the horizontal portion, and the buccal surface of the quadrate ramus are covered with irregularsized, randomly scattered denticles. In many specimens, the posterior region of the horizontal part shows extensive, irregular patches of worn dentine that are apparently deposited on top of worn teeth. These were interpreted by SMITH & CHANG (1990) as reparative tissue, and as a tissue unique to dipnoans (syndentine). All worn dentine surfaces in *Diabolepis* show a punctate pattern of rings of circumpulpal dentine (SMITH & CHANG, 1990, Fig. 4E). The circumpulpal dentine and associated interstitial dentine are also considered to be restricted to dipnoans (SMITH *et al.*, 1984). A left pterygoid (V9530) and a left lower jaw tooth plate (V9531) of very small size were found by WANG Nienzhong while sorting acidprepared microvertebrates from the *Diabolepis*-bearing locality. The pterygoid plate (Fig. 7A, B) is similar in shape and proportion to the larger (adult) plates. Its length from the anteromedial angle to the distal end of the quadrate ramus is approximately 2.7 mm, and its width from the anterolateral corner to the medial margin is 1.2 mm. This size falls near to the lower jaw tooth plate of a juvenile *Neoceratodus forsteri* described by KEMP (1979, Fig. 14C)

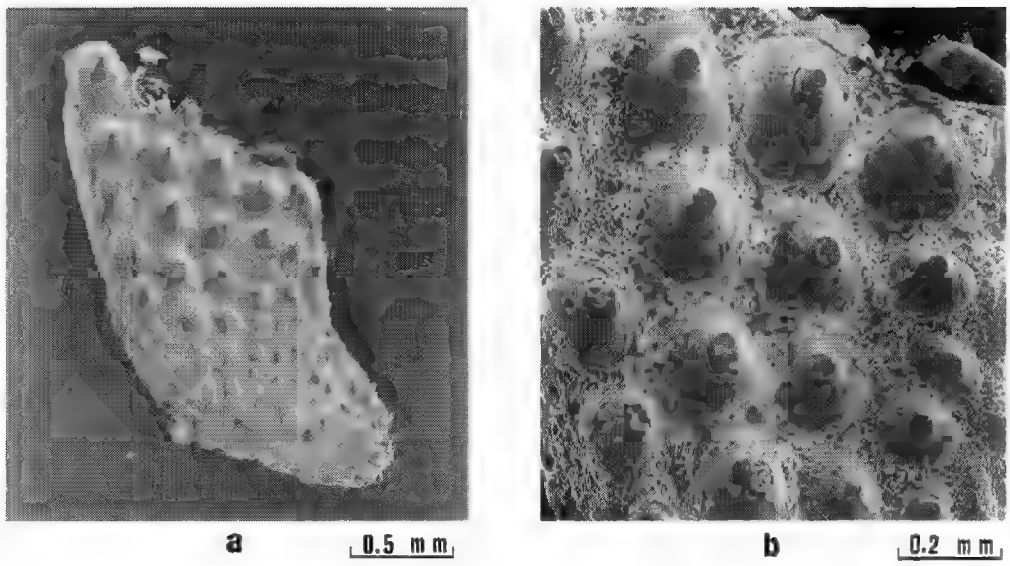

FIG. 7. — *Diabolepis speratus* (CHANG & YU), Lower Devonian, Yunnan, China. Pterygoid tooth plate in ventral view (A) and enlarged portion showing traces of wear (A), V9530.

Diabolepis speratus *(CHANG & YU), Dévonien inférieur, Yunnan, Chine. Plaque dentaire ptérygoïdienne en vue ventrale (A) et portion agrandie montrant des traces d'usure (B). V9530.*

with a body length of 8.7 cm and this pterygoid might belong to a juvenile individual of comparable size. The plate is slightly concave in its middle part and covered by regularly arranged rows of teeth, and is thus similar to the larger pterygoid plates. As in these plates the teeth are arranged in radial rows with the center of radiation approximately in the middle of the postcromedial margin. However, rows of teeth parallel to the anterolateral (labial) margin can also be distinguished in the anterior part of the plate. This might imply that the teeth in each row were formed within the same period, *i.e.* they are of the same generation. The largest teeth are situated along the labial margin which indicates that new teeth were added from this margin (SMITH & CHANG, 1990). On the posterolateral part of the horizontal portion and the quadrate ramus the teeth become much smaller and lose their regular arrangement. The teeth are pointed especially in the anterior part of the plate. No small denticle are observed on this plate, between the regular rows of teeth or the extensive patches of worn dentine covering the tooth rows. All this shows that this small plate must be from a juvenile, although traces of wear are already shown on the teeth in the middle part of the plate. Wear of the occlusal surface of the tooth plates was also mentioned by KEMP (1979: 255, table 1) in juvenile (stage viii) *Neoceratodus forsteri*.

Palatoquadrate

The palatoquadrate of *Diabolepis* was not co-ossified with the neurocranium. It is firmly attached to the visceral side of the pterygoid plate, the latter forming its lateral, medial and

posteromedial margins, and therefore it is usually preserved with detached pterygoid plates. The intimate contact between the palatoquadrate and the pterygoid plate often makes it difficult to trace the boundary between them. This is why, in the preliminary description of *Diabolepis* (CHANG & YU, 1984), the palatoquadrate was not recognized, and its dorsal surface was taken as the visceral surface of the pterygoid plate. A recently collected pterygoid plate (V9055), without attached palatoquadrate (Fig. 8A), makes it possible to unravel the outline of the latter. The palatoquadrate consists of a broad anterior, horizontal portion overlying the horizontal part of the pterygoid plate, and a postero-ventrolaterally extending quadrate portion that overlies the quadrate ramus of the pterygoid plate. The orientation of the quadrate is difficult to judge, since its distal end is not preserved. But as far as we can see from the extent of the quadrate ramus it must have been roughly vertical. A small posterolateral, semicircular, thickened area of the pterygoid plate, just in front of the quadrate, is exposed lateral to the palatoquadrate in exactly the same way as the dorsal thickening on the visceral surface of the pterygoid plate in fossil dipnoans (Fig. 8B; MILES, 1977, Figs. 76, 77 etc.). It differs only in its smaller size and more posterior position. In *Dipnorhychus sussmilchi* it was reported that the palatoquadrate and pterygoid are tightly fused, so that it is difficult to separate the two bones (THOMSON & CAMPBELL, 1971: 66). However, a figure in CAMPBELL & BARWICK (1982, Fig. 15a) and a specimen (BMNH,

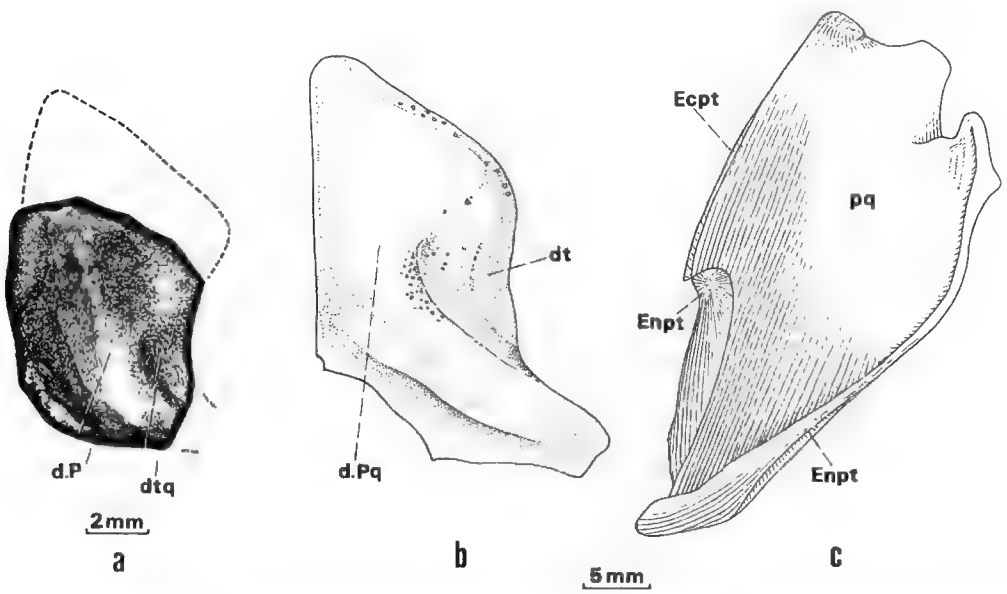

FIG. 8. — A, *Diabolepis speratus* (CHANG & YU), Lower Devonian, Yunnan, China; incomplete pterygoid tooth plate in visceral view, V9055. B, *Chirodipterus*, Upper Devonian of Australia, pterygoid tooth plate in visceral view (modified from MILES, 1977, Fig. 76a). C, *Glyptolepis*, *Middle Devonian of Greenland*, palatoquadrate with associated dermal bones in visceral view (from JARVIK, 1972, Fig. 25A).

A, Diabolepis speratus *(CHANG & YU), Dévonien inférieur, Yunnan, Chine. B*, Chirodipterus, *Dévonien supérieur d'Australie ; plaque dentaire ptérygoïdienne incomplète en vue viscérale (d'après MILES, 1977, fig. 76a, modifié). C*, Glyptolepis, *Dévonien moyen du Groenland, palatoarré et os dermiques associés en vue viscérale (d'après JARVIK, 1972, fig. 25A).*

P. 33699) clearly show a suture between the exposed area of the pterygoid and the palatoquadrate in this species. Judging from the smooth and concave posterior part of the lateral margin of the pterygoid in *Uranolophus* (DENISON, 1968, Figs. 8, 9), a small exposed area of the pterygoid might also exist in this region. The condition in *Diabolepis* also recalls that in porolepiforms, e.g. *Glyptolepis groenlandica* (Fig. 8C, JARVIK 1972, Fig. 25A), where the exposed area of the entopterygoid plate is small and posteriorly positioned. The entopterygoid bordering the posterolateral margin of the palatoquadrate has been described in almost all sarcopterygians, e.g. *Eusthenopteron* (for osteolepiforms; Fig. 9A; JARVIK, 1980, Fig. 107A), *Glyptolepis*, *Holoptychius* (for porolepiforms; JARVIK, 1972, Fig. 33B, E). In these two groups this exposed area is very smooth, probably to allow contraction of the adductor muscles passing from the palatoquadrate to the lower jaw (JARVIK, 1980: 174). In coelacanths, due to the lack of the commissural lamina of the palatoquadrate, almost the entire dorsal surface of the entopterygoid is exposed in lateral view (Fig. 9B; JARVIK, 1980, Figs. 218, 219). In early tetrapods, such as *Ichthyostega*, the dorsal surface of the palate has never been observed. As far as we can judge from its ventral surface (JARVIK, 1980, Fig. 171B), its posterolateral margin would also be bordered by the entopterygoid.

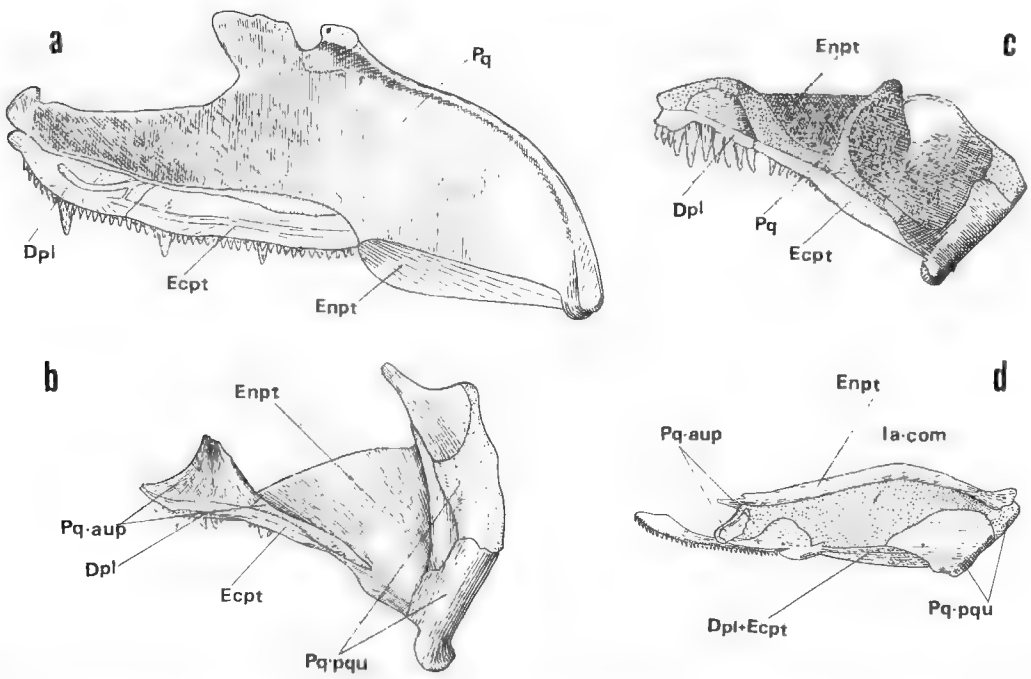

FIG. 9. — Palatoquadrate with associated dermal bones in lateral view. A, *Eusthenopteron*, Late Devonian of Canada (from JARVIK, 1980, Fig. 107A); B, *Latimeria*, Recent (from JARVIK, 1980, Fig. 219); C, *Amia*, Recent (from JARVIK, 1980, Fig. 40A); D, *Polypterus*, Recent (from JARVIK, 1980, Fig. 234C).

Palatocarré et os dermiques associés en vue latérale. A, Eusthenopteron, *Dévonien supérieur du Canada (d'après* JARVIK, *1980, fig. 107A) ; B,* Latimeria, *actuel (d'après* JARVIK, *1980, fig. 219) ; C,* Amia, *actuel (d'après* JARVIK, *1980, fig. 40A) ; D,* Polypterus, *actuel (d'après* JARVIK, *1980, fig. 234C).*

In actinopterygians (Fig. 9C) and *Polypterus* (Fig. 9D), on the contrary, it is not the entopterygoid but the ectopterygoid which borders the posterolateral margin of the palatoquadrate. The entopterygoid and dermometapterygoid in these forms cover only the medial portion of the ventral surface of the palatoquadrate (JARVIK, 1980, Figs. 40A, 234C, 236, 245B). In sarcopterygians the ectopterygoid and dermopalatine covers the anterolateral, but never the posterolateral margin of the palatoquadrate. An area of the entopterygoid exposed lateral to the posterolateral margin of the palatoquadrate seems thus to be a sarcopterygian character.

The anterior, horizontal portion of the palatoquadrate in *Diabolepis* is flat and broad and, on the whole, follows the outline of the pterygoid plate, although it is much narrower than the pterygoid, owing to the thick medial and posteromedial rims formed by the latter. A striking, unique feature is the sharp, transverse ridge on the middle part of the dorsal surface of the horizontal portion of the palatoquadrate. This ridge arises near the anterolateral corner of the palatoquadrate, extends medially, and then bends slightly posteromedially to merge with a strong process at the medial margin of the palatoquadrate. The only structure which is at all similar is the dorsal palatal process in *Uranolophus* (DENISON, 1968, Fig. 4), *Dipnorhynchus* (WHITE, 1965; BMNH P. 33699; THOMSON & CAMPBELL, 1971, "lateral palatal process", Fig. 26; CAMPBELL & BARWICK, 1982, "dorsal palatal process", Fig. 14) and *Stomiahykus* (BERNACSEK, 1977: 194, Figs. 8, 9) (Fig. 10). This process was regarded as endoskeletal by DENISON (1968: 374) and THOMSON & CAMPBELL (1971: 68). MILES, on the contrary, seemed to consider the process as exoskeletal. He named it the dorsal process of the entopterygoid and described it as arising from the top of a dorsal thickening comparable with the dorsal thickening on the pterygoid plate of *Chirodipterus* and other advanced dipnoans (MILES, 1977: 174; Figs. 76, 77). MILES

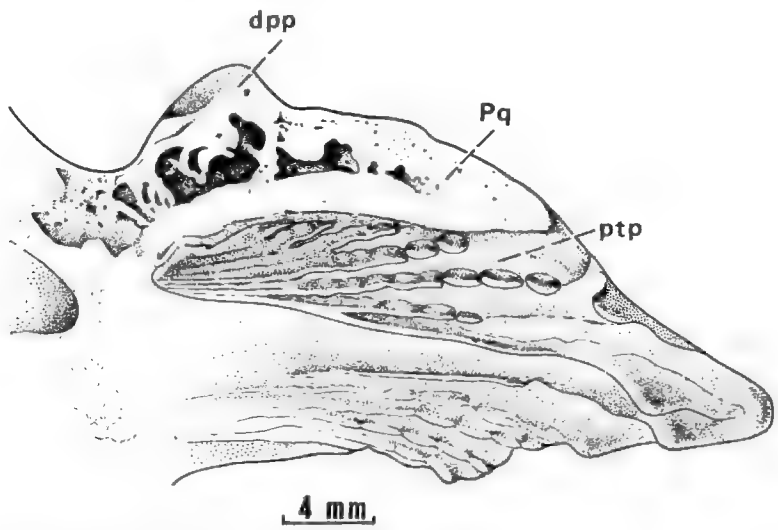

FIG. 10. — *Stomiahykus thlaodus* Bernacsek, Middle Devonian of Canada. Palate in right ventrolateral view showing the pterygoid tooth plates and palatoquadrate with broken right margin, NMC 22600.

Stomiahykus thlaodus *Bernacsek, Dévonien moyen du Canada. Palais en vue ventrolatérale droite, montrant les plaques dentaires ptérygoïdiennes et le palatocarré, dont le bord droit est brisé, NMC 22600.*

further compared this process with the short ascending process of the pterygoid plate in *Gnathorhiza* which, according to BERMAN (1976: 1026), articulated with the lateral surface of the broad, flange-like descending process of the skull roof, *i.e.* bone K-M, and tended to regard the dorsal and ascending processes throughout fossil and recent dipnoans as homologous. The descending process from the skull roof and the ascending process from the pterygoid plate in Recent dipnoans are undoubtedly exoskeletal. So are the processes of the same name in *Gnathorhiza*, as far as it can be understood from BERMAN (1976). In the preliminary description of *Diabolepis* (CHANG & YU, 1984), since the palatoquadrate was not recognized, the dorsal transverse ridge of the palatoquadrate was interpreted as comparable to the dorsal thickening (= the exposed area of the entopterygoid) on the visceral surface of the entopterygoid plate. Until the pterygoid plate without the palatoquadrate attached (V9055) was found, it was not realized that the dorsal thickening of the entopterygoid in *Diabolepis* (and probably also in *Dipnorhynchus* and *Uranolophus*) is very small and situated posteriorly. Consequently, the dorsal process (or ridge) of the palatoquadrate and the dorsal thickening of the entopterygoid are two different things. The former is an endoskeletal process on the lateral part of the palatoquadrate, whereas the latter is a thickened area of the entopterygoid exposed laterally to the posterolateral margin of the palatoquadrate and situated behind the former. A dorsal process (or ridge) of the palatoquadrate has been found in *Dipnorhynchus*, *Uranolophus*, *Stomiahykus* and *Diabolepis*. As to its function, nothing new can be added.

Anterior to the transverse dorsal ridge and anterolateral to the strong process at the medial margin of the palatoquadrate mentioned above is an elongated ridgelike process which has an anterolateral-posteromedial orientation, reaching the anterolateral margin of the palatoquadrate. On the anteromedial side of the ridge, overlying the anteromedial part of the pterygoid plate, is a thin lamina of the palatoquadrate which may be comparable with the anteromedial articular lamina of the palatoquadrate in porolepiforms, e.g. in *Glyptolepis* (JARVIK, 1972, Fig. 25). If we assume that the pterygoid plate with the palatoquadrate is situated on the side of the parasphenoid, so that the slightly convex medial margin of the pterygoid plate matches the slightly concave lateral margin of the parasphenoid, and that the protruded anteromedial corner of the pterygoid plate fits into the space lined medially and anteriorly by the parasphenoid and the vomer, then the strong process and the ridge mentioned above on the palatoquadrate are received by the suborbital fossa under the lateral border of the ventral surface of the neurocranium and the elongated fossa on the crista suspendens respectively. The thin, anteromedial lamina of the palatoquadrate fits in the fossa palatina (Fig. 11). Since the bottom of the suborbital fossa is not periosteally lined there is still the possibility of fusion or synchondrosis between the palatoquadrate and the neurocranium in this region. An articulation between the palatoquadrate and the lateral portion of the postnasal wall, like that in porolepiforms and probably *Eusthenopteron*, cannot exist, since the ventral surface of the postnasal wall is smooth and the anterior margin of the palatoquadrate, in this position, is situated some distance behind the postnasal wall. The two articulations described here in *Diabolepis* resemble the two special buttressing regions in the palatebraincase contact described by THOMSON & CAMPBELL (1971: 66) in *Dipnorhynchus*. One of those is a buttress of the palate under the root of the postnasal wall, and the other is a thickening of the visceral palate immediately anterior to the optic nerve foramen. As in *Dipnorhynchus*, the dorsal surface of the palate in *Uranolophus* is also thickened to buttress the

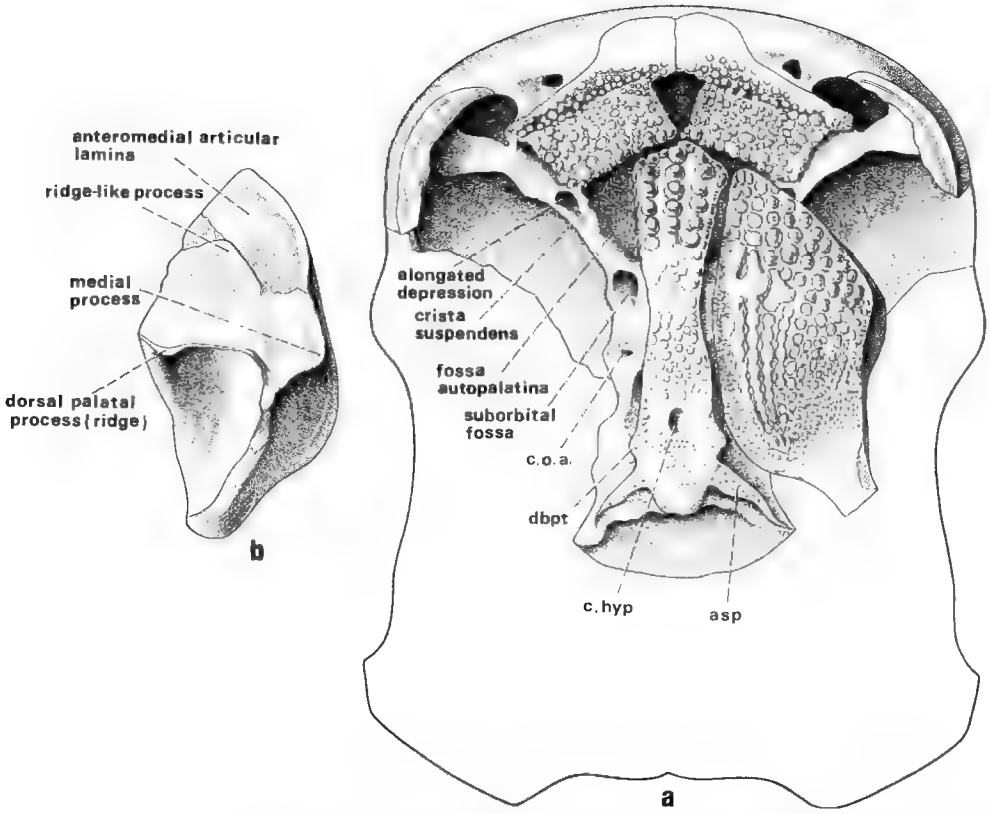

FIG. 11. — *Diabolepis speratus* (CHANG & YU), Lower Devonian, Yunnan, China. A, partial reconstruction of ventral side of the anterior portion of the cranium with the left pterygoid tooth plate *in situ*, based on specimens V7237, 7239, 7240 and 9054. B, pterygoid tooth plate with palatoquadrate in visceral view, V9054.

Diabolepis speratus *(CHANG & YU), Dévonien inférieur, Yunnan, Chine. A, reconstitution partielle de la portion antérieure du crâne, avec la plaque dentaire ptérygoïdienne gauche en position anatomique, d'après les spécimens V7237, 7239, 7240 et 9054. B, plaque dentaire ptérygoïdienne avec palatocarré en vue viscérale, V9054.*

braincase underneath the postnasal wall and just in front of the optic foramen (THOMSON & CAMPBELL, 1971: 81). With the pterygoid plate and the palatoquadrate thus applied against the neurocranium, the groove following the opening on the lateral wall of the neurocranium, behind the suborbital fossa (in V7240) is, situated between the ventral wall of the braincase and the palatoquadrate, and if the two were to fuse, a canal would be formed which opens at the bottom of the orbit. This is the condition in *Dipnorhynchus sussmilchi*, where a distinct ridge on the dorsal surface of the palate can be seen before the canal for the ophthalmic artery opens anteromedially to the dorsal process of the palatoquadrate (THOMSON & CAMPBELL, 1971: 68; CAMPBELL & BARWICK, 1982, Fig. 16).

It is generally accepted that in Recent and fossil adult dipnoans, the palatoquadrate is fused with the neurocranium through three processes, the otic process to the otic region; and the basal and ascending processes to the posterior part of the orbitotemporal region. It is also accepted that there is a strong pars pterygoquadrata but no pars autopalatina in dipnoans. According to BERTMAR's study of the embryology of *Neoceratodus* (1965), a processus pterygoideus of the palatoquadrate is developed in the 11.5 mm and 14.5 mm stages. However, it never chondrifies but forms a ligament at the 16 mm stage (p. 89). MILES (1971: 103) could not trace anything comparable to the pterygoid process in fossil dipnoans. JARVIK (1980: 400-402), however, suggested that the pars autopalatina in dipnoans was incorporated in the neurocranium, based on an assumed relationship of dipnoans with sharks.

A comparison of the palatoquadrate of *Diabolepis* with those of early fossil dipnoans, *i.e. Dipnorhynchus* & *Uranolophus*, supports JARVIK's suggestion that the pars autopalatina is still present in primitive fossil dipnoans. In specimens of *Diabolepis* the palatoquadrate is never co-ossified with the neurocranium but is attached to the visceral surface of the pterygoid plate. It is well-developed in having a pars autopalatina and a pars quadrata with a commissural lamina between them. The dorsal palatal ridge seems to be connected with the commissural lamina. There is no lateral ethmoidal articular process on the palatoquadrate, but the medial one is present in the form of the oblique ridge and the anteromedial articular lamina. There is a strong suborbital articulation. The equivalent articulation in other fishes cannot be decided at the moment, though MAISEY (1986) suggested it is no more variable than the orbital articulation among recent squalomorphs. Judging from the normally developed basipterygoid process, a basal process must be present on the palatoquadrate. In early fossil dipnoans such as *Dipnorhynchus* and *Uranolophus* the pars autopalatina and the commissural lamina must also be present, *i.e.* the part situated at, and lateral to, the buttress under the root of the postnasal wall, the part with the thickening under the optic foramen, and the part bearing the dorsal palatal process. These parts fuse with the ventral wall of the neurocranium, adding to the suborbital ledge and making it much broader than in other osteichthyans. In later dipnoans, though there is no direct evidence for this, the broad lateral extension of the suborbital ledge and the shape of the impression left by the ventral face of the neurocranium on the visceral surface of the pterygoid plates suggest that the pars autopalatina, and probably the commissural lamina, might be present and incorporated in the neurocranium. The difference between early and later dipnoans is that the dorsal palatal process is absent in the later, as is possibly the adjacent part of the palatoquadrate. This is probably the reason why the exposed area of the entopterygoid in later forms is more extensive and situated more anteriorly.

It is of interest to compare the palatoquadrate of *Diabolepis* with that of *Powichthys*, *Glyptolepis* (porolepiforms) and *Eusthenopteron* (osteolepiforms). In *Powichthys*, as in *Diabolepis*, the ventral surface of the postnasal wall is smooth and there can be no lateral ethmoidal articulation. However, the medial ethmoidal articulation is rather strong, with a well-defined bean-shaped area devoid of periosteal lining on the neurocranium and an ethmoidal process on the palatoquadrate (JESSEN, 1989, Figs. 4, 5; Pls 1.1, 2). According to JESSEN (1980: 199), the fossa autopalatina in *Powichthys* is not as well-developed as in *Porolepis*, *Holoptychius* and *Glyptolepis*, but a sufficiently well-developed anteromedial articular lamina is present in the detached palatoquadrates associated with *Powichthys*, that JESSEN (1980: 182) referred to porolepiforms.

The otic shelf in *Powichthys* (p. 205) decreases in breadth anteriorly and there is no possibility for such a paratemporal articulation as in *Eusthenopteron*. Judging from the well-developed basipterygoid process, a basal process must be present in *Powichthys*.

No palatoquadrate has been found in *Youngolepis*. On the evidence of the neurocranium, however, a palatoquadrate similar to that of *Powichthys* can be suggested. That is, there must be a palatoquadrate with the ethmoidal articulation concentrated in the medial side of the postnasal wall, and formed by articulations between the well-defined articular area and the fossa autopalatina of the neurocranium on the one hand, and the ethmoidal process and the anteromedial articular lamina of the palatoquadrate on the other. A basal process must also be present in *Youngolepis*, judging from the structure of the basipterygoid process. For the same reason as in *Powichthys*, there can be no paratemporal articulation. Since there is no suprapterygoid process in *Youngolepis* or *Powichthys*, it is difficult to infer whether an ascending process was connected to the palatoquadrate or not. In the detached palatoquadrate associated with *Powichthys*, however, a rather extensive processus ascendens with ridges for attachment of muscles was indicated by JESSEN (1980, Figs. 1, 2; Pl. 1).

The palatoquadrate in porolepiforms shows an ethmoidal articulation with the postnasal wall on its lateral side, unlike that in *Diabolepis*, *Powichthys* and *Youngolepis*. Although there is no well-defined area comparable to that in *Youngolepis* and *Powichthys* for the medial articulation, there is always a fossa autopalatina in various degree of development received the rather extensive anteromedial articular lamina of the palatoquadrate. A basal articulation must also be present. The grinding series of *Glyptolepis groenlandica* shows a fusion in all these areas (JARVIK, 1972: 57; BJERRING, 1989, Figs. 2A, 3B). Since there is no articular area without periosteal lining on the ascending process, it is suggested by JARVIK (1972: 71) that there was only a ligamentous connection between the ascending process and the suprapterygoid process. As in *Youngolepis* and *Powichthys*, the otic shelf is concave ventrally and decreases in breadth anteriorly, and the paratemporal articulation is absent.

In *Eusthenopteron* the palatoquadrate is, on the whole, similar to that of porolepiforms. However, it has a strong apical process which fits into the well-defined articular area in the medial side of the postnasal wall, lacks the anteromedial articular lamina and the related fossa autopalatina on the neurocranium, has a better formed articulation between the ascending process and the suprapterygoid process, and has a paratemporal process for articulation with the thick anterior end of the otic shelf. The latter seems to be an autapomorphy of *Eusthenopteron* (or osteolepiforms).

Lower jaw

The lower jaw of *Diabolepis* is the part of its skull that is most suggestive of dipnoans. The main reason why CAMPBELL & BARWICK (1987: 36) doubted that *Diabolepis* was a dipnoan was the uncertainty as to whether the lower jaw, pterygoids and cranium belonged to the same animal. The structure of the lower jaw of *Diabolepis* is, in general, very similar to that of tooth platebearing dipnoans. It shows, on its external face, a comparatively short dentary and four infradentaries lying in a row (as in early dipnoans). It is almost impossible to trace the sutures between these bones because of the cosmine covering. In only one specimen, V7248, where the superficial bone layer is worn away, can the boundaries between the four infradentaries be made

out by following the sutures and the lines radiating from the centres of the bones (Fig. 12). A short, posterior division of the suture between the dentary and infradentary 4 can be seen on V7248, whereas the rest of the suture can only be estimated according to the dorsal extent of the sutures between the infradentaries and the radiation of their bone structures. The inflected dorsal portion of the dentary is covered with small teeth which are not arranged in one row along the margin, but scattered to form a tooth patch, probably occluding with the tooth band on the anterior portion of the upper jaw formed by the premaxillary and vomerine teeth. In other dipnoans the dentary is usually not a toothbearing bone, except in a few forms where tubercles or rows of tubercles are observed on its lateral margin (e.g. *Griphognathus*; MILES, 1977, Fig. 98; *Uranolophus*, DENISON, 1968, Fig. 14A). The labial tooth plates (SEMON, 1899) which appear in early embryonic stages of *Neoceratodus* degenerate at a later stage and finally disappear, and may indicate the presence of a toothbearing dentary in the early phylogeny of dipnoans. Behind the inflected toothbearing portion, the dentary of *Diabolepis* extends further backwards along the lower border of the labial pit and the lower jaw margin in the form of a long, narrow strip. It ends at a point dorsal to the anterior part of infradentary 4, lateral to the

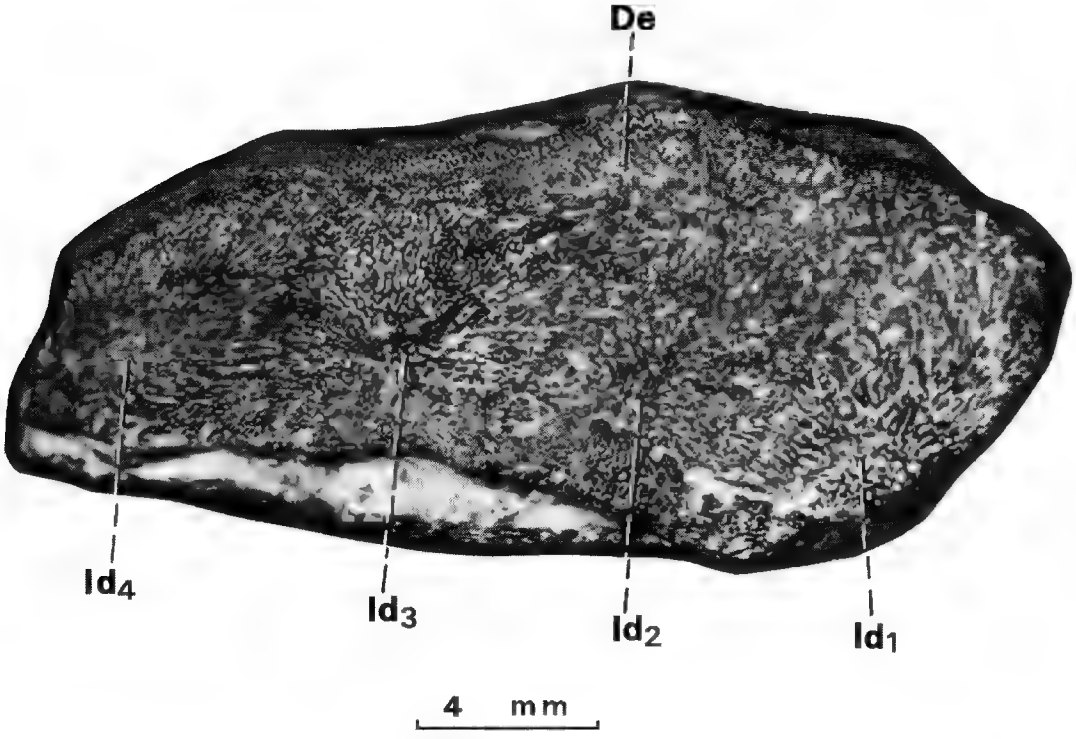

FIG. 12. — *Diabolepis speratus* (CHANG & YU), Lower Devonian, Yunnan, China. Right lower jaw rami in external view, V7248.
Diabolepis speratus *(CHANG & YU), Dévonien inférieur, Yunnan, Chine. Branche droite de la mandibule en vue externe, V7248.*

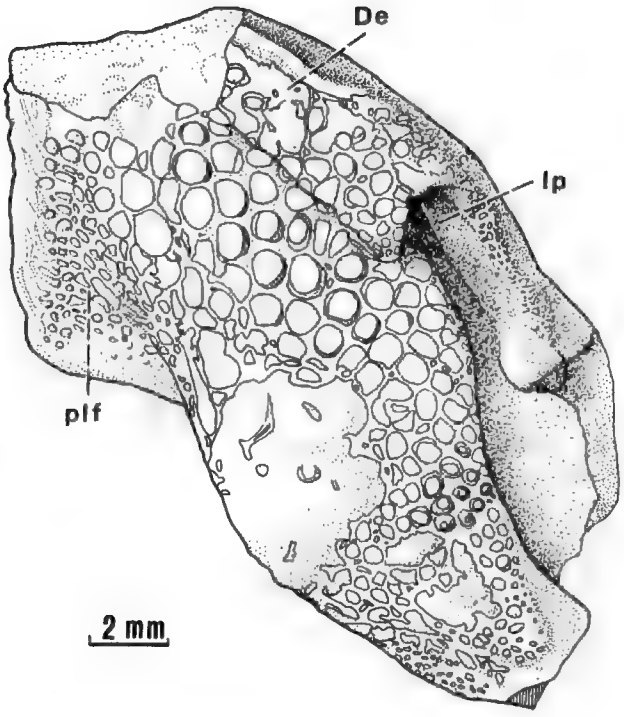

FIG. 13. — *Diabolepis speratus* (CHANG & YU), Lower Devonian, Yunnan, China. Right lower jaw rami in buccal view, V9527.

Diabolepis speratus *(CHANG & YU), Dévonien inférieur, Yunnan, Chine. Branche droite de la mandibule en vue buccale, V9527.*

posterior part of the lower tooth plate and the adductor fossa. This narrow, posterior extension of the dentary is divided into two longitudinal portions, a lateral one covered with cosmine and a medial one devoid of cosmine. In a specimen (V9529, Fig. 13) newly collected by FAN Junhang, the upper (inner) border of the cosmine-covered portion bears numerous denticles with shiny surfaces. In V7248, no signs of denticles or teeth are seen along the corresponding border, but broken, irregular tooth-like structures can be seen along the inner margin of the portion devoid of cosmine. In V7249, as in most other dipnoans, the lower jaw margin behind the inflected part of the dentary, either the cosmine-covered part or the part devoid of cosmine, lacks any kind of teeth or denticles. In V7248 the distal portion of the cosmine-covered part of the dentary is slightly expanded. This small, oval portion resembles the small rounded piece of cosmine-covered bone occupying a similar position in V7249 (CHANG & YU, 1984, Fig. 5B; SMITH & CHANG, 1990, Fig. 1B). It seems that this small piece of bone in V7249 is the broken, distal, expanded end of the cosmine-covered part of dentary (Fig. 14). On the internal (buccal) side of the lower jaw there is only one extensive dermal bone, the prearticular (but see SMITH & CHANG, 1990), that is entirely covered with teeth or denticles, as is the case with its opposing bone in the upper jaw, the pterygoid plate. The dorsal surface of the prearticular is rhombic in shape and differentiated from the rest of the plate. It is on the whole convex (e.g. in V7247 and V7249), so as to match the reciprocally concave ventral surface of the pterygoid plate, although the convexity is much less conspicuous in some specimens (e.g. V7248 and V9529) where the

teeth are worn. The dorsal surface of the prearticular is characterized by a regular arrangement of teeth in radiating rows. The tooth rows converge in a posteromedial direction and the worn teeth fuse at the posteromedial corner of the dorsal face to from a patch of continuous, worn dentine resembling the heel of the tooth plate in later dipnoans such as *Speonesydrion*, *Holodipterus* and *Dipterus*. All this makes the prearticular closely resemble the tooth plate of later dipnoans with only two differences.

1 – Not only the dorsal surface but also the remaining part of the bone, from the symphyseal portion along the entire lingual side to the area around the glenoid fossa, is covered with small, randomly scattered denticles. In most dipnoans with tooth plates, the parts of the pterygoid that are not covered by the tooth plates are usually smooth, although denticles in the lingual groove (prolingual field) and around the inner and posterior margin of the tooth plates are seen in *Speonesydrion* (CAMPBELL & BARWICK, 1984, Fig. 30). A prearticular extensively covered with denticles is also found in *Uranolophus* (DENISON, 1968, Fig. 14) and *Griphognathus* (MILES, 1977, Figs. 98, 100b), although the area of bone lateral to the tooth ridge in the former and below the denticulated area in the latter is still smooth. In *Glyptolepis* the prolingual field, an

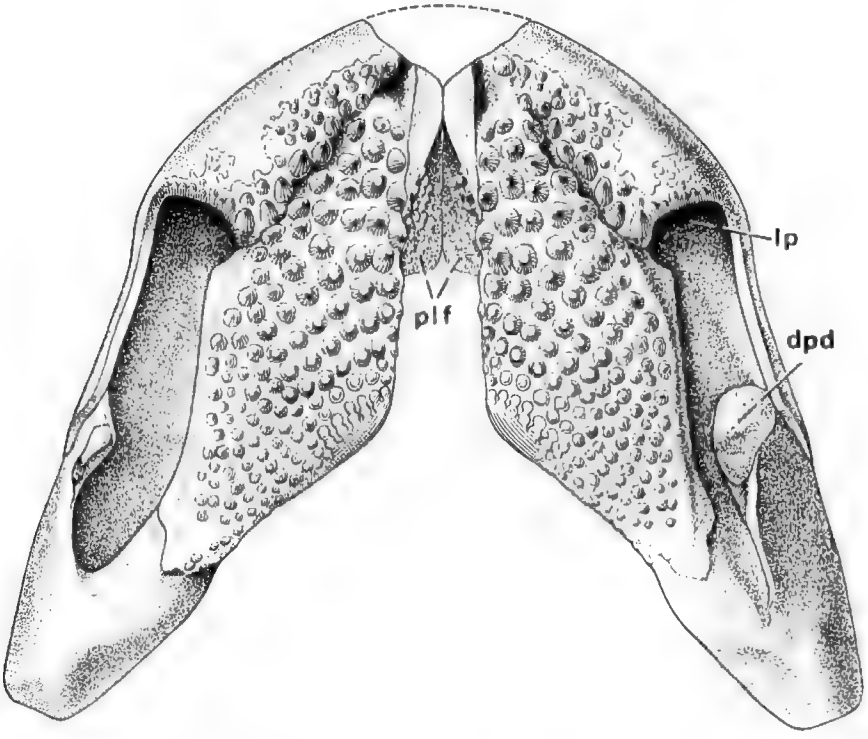

FIG. 14. — *Diabolepis speratus* (CHANG & YU), Lower Devonian, Yunnan, China. Tentative reconstruction of lower jaw in dorsal view, mainly based on V7248 and V7249.

Diabolepis speratus *(CHANG & YU), Dévonien inférieur, Yunnan, Chine. Essai de reconstitution de la mandibule en vue dorsale, d'après principalement les spécimens V7248 et V7249.*

area approximately corresponding to the lingual groove in dipnoans, is covered with numerous small dental plates (JARVIK, 1963, Figs. 14A-B, 15A-B), but no dental plates below the denticulated area of the prearticular were shown by the grinding series.

2 – No adsymphysial plate like that present in many other dipnoans, e.g. *Griphognathus, Chirodipterus, Holodipterus, Rhynchodipterus, Dipterus*, has been observed in *Diabolepis*.

The posterior portion of the lower jaw ramus is much more slender than its anterior portion or the corresponding portion in other dipnoans. The adductor fossa is of the usual dipnoan type. It is small and narrow, somewhat slit-like and flanked by the prearticular medially, and the dentary and infradentary 4 laterally. Behind the fossa, in V7249, the dermal bones of both external and internal sides extend up and then towards each other to form the posterolateral border of the adductor fossa. The glenoid fossa is not preserved. Since the posterior portion of the lower jaw is thin, the articulation for the quadrate cannot be very strong. This seems to accord with the slender quadrate. On the lateral side of the lower jaw, behind the tooth-bearing portion of the dentary, is the labial pit, which is characteristic for dipnoans.

The small prearticular tooth plate (Fig. 15), found by WANG Nienzhong (V9531), falls in the same size range as the juvenile lower jaw tooth plate mentioned above (KEMP, 1979, Fig. 14C), with a length of 2.9 mm and a width of 1.1 mm. The plate shows slight differences in shape, proportions and arrangement of teeth from those of the larger (adult) plates. The occlusal surface of the entire plate is notably convex. However, unlike the adult plates, there is no well-defined, rhombic, dorsal portion differentiated from the rest of the plate. No particularly regular

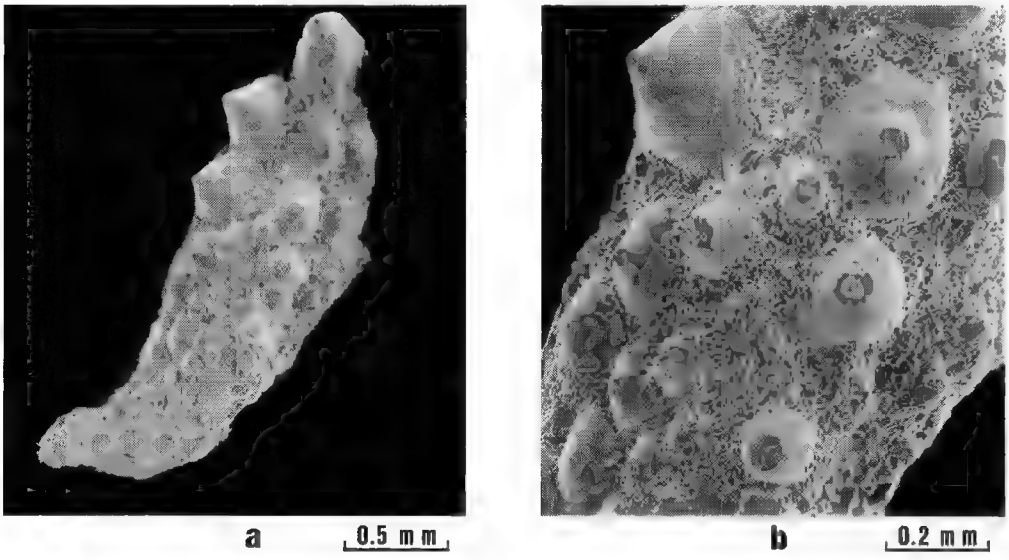

FIG. 15. — *Diabolepis speratus* (CHANG & YU), Lower Devonian, Yunnan, China. Prearticular tooth plate in buccal view (A) and enlarged portion showing traces of wear (B). V9531.

Diabolepis speratus *(CHANG & YU), Dévonien inférieur, Yunnan, Chine. Plaque dentaire préarticulaire en vue buccale (A) et portion agrandie montrant des traces d'usure (B), V9531.*

pattern of tooth arrangement could be made out. Three conspicuous, pointed teeth are situated at the anterolateral (labial) margin, which might give some hint of the growth pattern of the plate, *i.e.* new teeth added from the labial margin, as mentioned by SMITH & CHANG (1990). The teeth in the middle part of the plate bear faint traces of wear.

DISCUSSION AND CONCLUSIONS

The characters of *Diabolepis* described above and their distribution in other sarcopterygians are summarized in the following table (table 1).

The characters used in table 1 are:

1. Appearance of median bone in skull roof.

2. Numerous bones carrying the supraorbital sensory canal.

3. Anterior mosaic in skull roof.

4. Premaxilla independent.

5. Westoll-lines.

6. Interruption of the infraorbital sensory canal at anterior nostril.

7. Cosmine present.

8. Main lateral-line canal running along edge of supratemporal series.

9. Posterior elements of the nasal series and anterior elements of the supratemporal series lying side by side.

10. Fenestra ventrolateralis present.

11. Vomerine area with uneven surface divided by grooves into raised areas of irregular shape and size.

12. "Rostral tubuli".

13. Tectum orbitale extensive.

14. Suborbital articulation between palatoquadrate and neurocranium.

15. Basipterygoid process laterally expanded.

16. Part of ophthalmic artery canal between ventral wall of braincase and palatoquadrate.

17. Medial ethmoidal articulation between the anteromedial articular lamina of the palatoquadrate and the fossa autopalatina of the neurocranium.

18. Vomers separated from each other.

19. Dorsal palatal process (ridge) present.

20. Marginal teeth reduced, teeth on premaxilla and dentary, if present, never consisting of a single row of conical teeth.

21. Labial pit.

22. Small number of dermal bones covering the palate and the lingual side of the lower jaw.

23. Regular arrangement of the teeth (radial rows) on the dorsal surface of the prearticular and the ventral suface of the pterygoid.

24. Prolingual field covered with denticles.

25. Syndentine, circumpulpal dentine, and associated interstitial dentine.

The characters chosen here are all present in *Diabolepis* and restricted to the head region, many characters occurring in other sarcopterygian groups, but not present in *Diabolepis*, are not included. It is obvious from the table that *Diabolepis* and dipnoans share most characters (1-25). Among them ten (1, 5, 14, 16, 19-23, 25) are uniquely shared. Alhough characters 14, 15, 17 are used with the assumption that the articulations were fused in dipnoans and character 17 deserves observation on more specimens to be confirmed, the rest are well understood through extensive comparison. The ten characters mentioned above are mainly related to the palatoquadrate, jaw and bite, while the cranium of *Diabolepis* shows quite a few primitive sarcopterygian or osteichthyan characters, e.g. the presence of a premaxilla; the excurrent nostril occupying a position lateral to the premaxilla; the long parasphenoid extending anteriorly to the ventral side of the ethmoidal region, separating the pterygoids in the midline and restricted only to the anterior cranial portion; the folded teeth; the otic region of the neurocranium entirely lined by the skull roof, leaving no space for any ridges or muscle insertion; the palatoquadrate not fused with the neurocranium; etc. It is precisely these primitive sarcopterygian characters which caused hesitation in placing *Diabolepis* among dipnoans. In spite of the few primitive characters seen on the pterygoid plate and the lower jaw (both pterygoid and prearticular extensively covered with teeth and denticles, dentary with teeth, and four infradentaries), they bear more dipnoan characters than the cranium and, on the whole, look more dipnoan-like. There has been little doubt in referring them to dipnoans. Now that the palatoquadrate and related parts of the neurocranium are better known, it is more certain that the parts mentioned above belong to the same animal. First, the ridge-like process and the stout process on the median margin of the dorsal surface of the palatoquadrate fit well into the elongated fossa on the ventral side of the crista suspendens and the suborbital fossa on the ventral wall of the braincase below the optic foramen. This relates the palatoquadrate and pterygoid plate to the cranium with certainty. Then, the palate and lingual surface of the lower jaw show a similar disposition of dermal bones, *i.e.* the toothed patch on the inwardly bending portion of the dentary corresponds to the toothed band on the anterior end of the upper jaw formed jointly by the premaxilla and vomer, and the dorsal surface of the prearticular corresponds to the ventral surface of the pterygoid. The surfaces of the last two bones are reciprocally curved to fit each other and are covered with similarly arranged, radiate rows of teeth. The wear pattern is also very similar. The worn tooth bases are coated with enamel, and the worn dentine shows the punctate pattern of rings of circumpulpal dentine seen in the lip tissue of *Griphognathus* (SMITH & CHANG, 1990). Thus, increased evidence suggest

TABLE 1. — Distribution of characters of *Diabolepis* in sarcopterygians. +, yes; –, no; F, suggested fusion between neurocranium and palatoquatrate; ?, data not available; N, not applicable.

Distribution des caractères de Diabolepis *chez les Sarcoptérygiens. +, présent ; -, absent ; F, fusion possible entre le neurocrâne et le palatocarré ; ?, donnée inconnue ; N, non appliquable.*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Actinopterygians	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eusthenopteron	-	-	-	-	-	-	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Porolepiforms	-	+	+	-	-	-	+	-	-	+	-	?	+	-	+	-	+	+	-	-	-	-	-	+	-
Powichthys	-	+	+	+	-	?	+	-	+	+	-	+	?	-	+	-	+	+	-	-	-	-	-	?	-
Youngolepis	-	?	?	+	-	+	+	+	+	+	+	+	+	-	+	-	+	+	-	-	-	-	-	?	-
Diabolepis	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Dipnoans	+	+	+	N	+	+	+	-	+	+	-	+	+	F	F	F	F	?	+	+	+	+	+	+	+
Cœlacanths	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tetrapods	-	-	-	-	-	-	-	-	-	+	-	-	-	N	N	-	N	-	-	-	-	-	-	-	-

that the cranium, pterygoid plate and lower jaw belong to the same form and the close relationship between *Diabolepis* and dipnoans suggested by uniquely shared derived characters is further strengthened.

The rest of characters shared by *Diabolepis* and dipnoans falls into two sets, one is shared by them and porolepiforms, *Powichthys*, and *Youngolepis*; the other is shared by them, *Powichthys*, and *Youngolepis*, or shared by *Diabolepis* and *Youngolepis* alone. The first set of characters includes 2, 3, 13, 15, 17, 18, and 24. In characters 15 and 17 the related parts of the palatoquadrate in dipnoans are assumed to be fused with the neurocranium, in characters 2 and 3 the bones carrying the supraorbital sensory canal and those of the anterior mosaic of the skull roof are suggested to be fused with each other in *Youngolepis*, and in 24 the state of the denticle covering in the prolingual field in *Youngolepis* and *Powichthys* is not yet known. However, these characters show a possible close relationship between porolepiforms, including *Powichthys* and *Youngolepis*, and dipnoans, including *Diabolepis*. The second set of characters includes 4, 6, 8, 9 and 11. They seem to group *Powichthys* and *Youngolepis* with *Diabolepis* and dipnoans or *Youngolepis* with *Diabolepis*.

If *Diabolepis* is to be included in the group Dipnoi, the definition of the group would certainly be changed and, consequently, a few characters supposed to be shared by dipnoans and tetrapods are to be deleted. As FOREY (1987: 84) pointed out, some fossils provide evidence that question some of the characters used to support the theory of lungfish / tetrapod sistergroup relationship. In the case of *Diabolepis*, the pterygoids meeting at the midline and the short parasphenoid would be taken away from the list of characters uniquely shared by dipnoans and tetrapods proposed by ROSEN *et al.* (1981). This often happens when a new taxon is discovered and its relation to known taxa is restored. To delete a few characters from, or to add a few to the definition of certain groups is not the only refinement that *Diabolepis* can offer. The most interesting change brought about by *Diabolepis*, considered together with *Youngolepis*, is to provide an alternative hypothesis for the interrelationships of sarcopterygians supported by evidence others than what we knew before. That is, the close relationship between dipnoans and porolepiforms, in contrast to the close relationship between dipnoans and tetrapods. When *Powichthys*, a much porolepiform-like "rhipidistian" was discovered from the Lower Devonian of the Arctic Canada (JESSEN, 1975), the similarities between it and dipnoans were already noticed by ROSEN *et al.* (1981: 165). The characters shared by *Powichthys*, *Youngolepis* and porolepiforms, *i.e.* a fossa autopalatina, foramen for the pituitary vein anterodorsal to the basipterygoid process, vomers widely separated by the internasal pits and parasphenoid, internasal ridge and much enlarged, downwardly pointing basipterygoid process, were indicated by GARDINER (1984: 404) to group them together. He further suggested a sister-group relationship between porolepiforms + *Youngolepis* and dipnoans + tetrapods (GARDINER, 1984, Fig. 147) on the basis of two characters, namely, the immobilization of the intracranial joint and the cosmine porecanal system in which the mesh canals are without a horizontal partition and the porecanals are enamel-lined. However, from the two characters the second one is shared only by porolepiforms and dipnoans (see also ROSEN *et al.*, 1981: 257). MAISEY (1986: 232-240; Fig. 14; see also JANVIER, 1986) was the first to note the porolepiform / dipnoan sister-group relationship. He started from the two characters mentioned by GARDINER and added the rostral tubuli and the dipnoan-like pectoral endoskeleton with a single series of "mesomeres" of *Glyptolepis* to show that

porolepiforms are a paraphyletic group of "stem dipnoans". The number of characters shared by porolepiforms and dipnoans has been increasing with further work on the newly discovered *Powichthys*, *Youngolepis* and *Diabolepis* as well as previously known sarcopterygians. From the four characters suggested for *Youngolepis*, *Powichthys* and porolepiforms by GARDINER, three (fossa autopalatina, vomers separated by internasal pit, and enlarged, downwardly pointing basipterygoid process) were observed in *Diabolepis*. The fourth, the position of the pituitary vein has yet to be found out in *Diabolepis*. A better understanding of known characters have been reached through examination of new specimens. The fossa autopalatina, as we now understand it, is the space for the anteromedial lamina of the palatoquadrate to insert or to articulate. New shared characters, such as the prolingual field covered with denticles, numerous bones carrying the supraorbital sensory canal, the anterior mosaic of the skull roof, etc, have been added. Close relationship between *Diabolepis* and dipnoans and the grouping of porolepiforms with dipnoans were shown in cladograms of sarcopterygians appeared in quite a few newly published papers (YU, 1990; CHANG, 1991; FOREY *et al.*, 1991; AHLBERG, 1991; CLOUTIER, 1992). SCHULTZE (1991, 1992) also accepts the sister-group relationship between *Diabolepis* and dipnoans, though not yet that between porolepiforms and dipnoans. With shared characters in regions others than the skull added, and analysis of character distribution in sarcopterygians as a whole, a clearer picture of the interrelationships of sarcopterygians can probably be obtained.

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A functional interpretation of the anteriormost vertebrae and skull of *Eusthenopteron*

by Edward C. HITCHCOCK

Abstract. — Mechanical preparation of a specimen of *Eusthenopteron foordi* has revealed the articulated anterior portion of the vertebral column, allowing for a comprehensive redescription and analysis of this region. Neural arches are smaller than more posterior trunk segments, and do not fuse dorsally as neural spines. Incipient zygapophyses occur lateral or ventrolateral to the nerve cord. Intercentra are paired, but do fuse in some specimens. Large blade-like supraneural spines are present above neural arches 1, 3, and 5, but not 2 or 4. The supraneural spines supported a muscular complex involved in feeding not only through raising the snout, but also by depression of the lower jaws induced by the forward swing of the quadrate. Flexion of the intracranial joint is likely responsible for the initiation of jaw closure during feeding

Keywords. — Vertebrata, Sarcopterygii, Osteolepiformes, Devonian, Canada, functional anatomy.

Interprétation fonctionnelle des vertèbres les plus antérieures et du crâne d'*Eusthenopteron*

Résumé. — La préparation mécanique d'un spécimen d'*Eusthenopteron foordi* a révélé la partie antérieure articulée de la colonne vertébrale, permettant ainsi une redescription et une analyse détaillées de cette région. Les arcs neuraux sont plus petits que dans les segments plus postérieurs du tronc et ne sont pas fusionnés dorsalement en épines neurales. Des ébauches de zygapophyses apparaissent latéralement ou ventro-latéralement à la moelle épinière. Les intercentres sont pairs, mais ne sont pas fusionnés sur certains spécimens. De grandes épines supraneurales en forme de lames sont présentes au-dessus des arcs neuraux 1, 3, et 5, mais absentes des arcs neuraux 2 et 4. Les épines supraneurales soutenaient un complexe musculaire mis en jeu dans la manducation, non seulement en relevant le museau, mais aussi en favorisant l'abaissement de la mandibule, induit par le basculement antérieur du carré. La flexion de l'articulation intracrânienne est vraisemblablement responsable du déclenchement de la fermeture de la bouche lors de la manducation.

Mots-clés. — Vertebrata, Sarcopterygii, Ostéolépiformes, Dévonien, Canada, anatomie fonctionnelle.

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INTRODUCTION

The osteolepiform rhipidistians are considered by most paleontologists to be the sister-group of tetrapods, or the group from which the tetrapods arose (WATSON, 1926; JARVIK, 1942; THOMSON, 1962; PANCHEN & SMITHSON, 1987; but for an alternate view see PATTERSON, 1980; ROSEN *et al.*, 1981). Any study of the origin of tetrapods must therefore rely heavily on knowledge of the osteolepiform rhipidistians. One character of tetrapods not present in fish is an atlas-axis

complex. In order to shed some light on the history of this structure the anteriormost vertebrae are examined in *Eusthenopteron,* which is one of the best known rhipidistians, thanks to the life work of Professor Erik JARVIK.

Previous descriptions of the anteriormost region of the vertebral column of *Eusthenopteron foordi* based on grinding series (JARVIK, 1975, 1980), and disarticulated remains (ANDREWS & WESTOLL, 1970), conflict with one another. My intent in this paper is to clarify this discrepancy by preparation and direct observation of a three dimensional skull of *Eusthenopteron* in which the anterior part of the vertebral column is intact, and determine the functional significance of these elements in conjunction with structures of the cranium. As this region is associated with the epaxial muscles involved in skull movement, this problem also involves the functional morphology of feeding mechanics in this fish.

Skull mobility and feeding mechanics have been studied previously in coelacanths (LAUDER, 1980; LUND *et al.*, 1985) and rhipidistians (THOMSON, 1967) in an effort to understand the role, if any, of a bipartite braincase in these groups. A different model is discussed in this paper, wherein the snout region is flexed at the initiation rather than at the end of jaw closure.

ABBREVIATIONS

ch	cheek plate, *plaque de la joue*;
Et	ethmosphenoid, *ethmosphénoïde*;
hb ap	hypobranchial apparatus, *appareil hypobranchial*;
Hsp	haemal spine, *épine hémale*;
Hy	hyomandibular, *hyomandibulaire*;
hyv	ventral facet for articulation with the hyomandibular, *facette ventrale pour l'articulation avec l'hyomandibulaire*;
Ic	intercentrum, *intercentre*;
Id	interdorsal, *interdorsal*;
jc	jugular canal, *canal jugal*;
l. com	lateral commissure, *commissure latérale*;
l.j	lower jaw, *mandibule*;
Na	neural arch, *arc neural*;
nc	notochord, *nôtocorde*;
nr.c	neural canal, *canal neural*;
Nsp	neural spine, *épine neurale*;
Occ	occiput, *occiput*;
Op	opercular, *operculaire*;
Ot	otoccipital, *otoccipital*;
p.o.m.add. hy	process for the origin of the adductor hyomandibularis, *processus pour l'attache du muscle adducteur de l'hyomandibulaire*;
Pc	pleurocentrum, *pleurocentre*;
Pq	palatoquadrate, *palatocarré*;
SN	supraneural, *supraneural*;
Sop	subopercular, *sous-operculaire*;
v Va	ventral vertebral arch, *arc vertébral ventral.*

MATERIALS AND METHODS

All the specimens of *Eusthenopteron* examined were collected from the Escuminac Formation on the Restigouche River, on the south coast of the Gaspé Peninsula, Quebec, Canada. This site is now a provincial park, Parc de Miguasha, and is the location of the Musée d'Histoire naturelle de Miguasha (MHNM).

The specimens used in this study are as follows:

— GN 790 (Cambridge University, Museum of Zoology). A short series of vertebrae.

— MHNM 06-216. An articulated series of trunk vertebrae.

— MHNM 06-12-196. The ventral half of the otoccipital portion of the endocranium.

— ROM 1234 (Royal Ontario Museum, Toronto, Canada). An endocranium, first described by STERNBERG (1941).

— ROM 1245. An almost complete vertebral column in ventral aspect with some skull bones.

— BMNH P. 6796a (The Natural History Museum, London, United Kingdom). A large three dimensional skull, behind which lies much postcranial material, mostly disarticulated.

— RM 14234 (Redpath Museum, McGill University, Montreal, Canada). A complete three dimensional skull. Mechanical preparation exposed the anterior portion of the vertebral column and the occiput. This specimen forms the basis of this research.

Mechanical preparation of RM 14234 and MHNM 06-12-196 was done using a Chicago Pneumatic CP-9361-1 Air Scribe. Delicate preparation was performed using a mounted needle. Some chemical preparation was done using 10% acetic acid. VINAC B-15 polyvinyl acetate was used as a consolidant.

RESULTS

OBSERVATIONS OF THE BRAINCASE OF *Eusthenopteron*

The anatomy of the braincase of *Eusthenopteron* has been previously described in great detail (JARVIK, 1954, 1980; BJERRING, 1971, 1978). During the course of this study some additional features were revealed.

Posterior and ventral to the jugular canal on the posterior face of the lateral commissure lies a process, presumably for the origin of the adductor hyomandibularis (BJERRING, 1971; JARVIK, 1980) which has not previously been described in detail. The lateral face of this process (Fig. 1) bears a groove continuous with the jugular canal. The dorsal margin of the process forms a slight ridge which extends anteriorly into the jugular canal, indicating that the vessels that passed through the jugular canal diverged. The course of one vessel passes medial to the process and follows the contour of the braincase, while the other passes between this process and the hyomandibular. A groove on the medial face of the proximal end of the hyomandibular, possibly for a large vessel, substantiates this. The jugular groove along the side of the braincase, which has been well documented (JARVIK, 1954; 1980), ends posteriorly at the lateral occipital fissure below the postotical process.

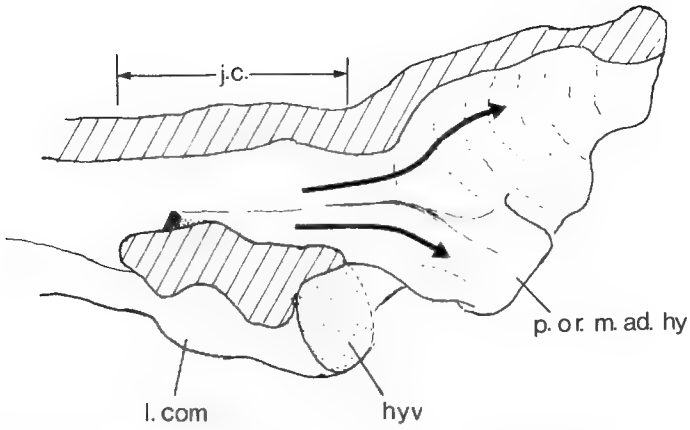

FIG. 1. — The left jugular canal of specimen MHNM 06-12-196 in dorsolateral view. Hatching indicates sectioned bone, and arrows indicate the direction of vessels leaving the canal posteriorly. (From HITCHCOCK, 1992, Fig. 4).

Canal jugulaire gauche du spécimen MHNM 06-12-196 en vue dorso-latérale. Les hachures indiquent l'os sectionné et les flèches indiquent la direction des vaisseaux quittant le canal postérieurement. (D'après HITCHCOCK, 1992, fig. 4).

Medial to the process for the origin of the adductor hyomandibularis, and extending anteriorly from the postotical process on the ventral surface of the parotic crest, is a conspicuous crescentic ridge (see the reconstruction in Fig. 7A). The ventral portion of this structure forms the dorsal margin of the jugular groove, and has been termed the jugular ridge (JARVIK, 1980). This was first documented in *Ectosteorhachis* (described as *Megalichthys*) (ROMER, 1937), and was interpreted as the origin for the adductor opercularis. This is corroborated by the position of origin of this muscle in *Latimeria* (MILLOT & ANTHONY, 1958). It lies dorsal to the origin of the adductor hyomandibularis and posterior to the dorsal articulation of the hyomandibular.

Ventral to the jugular groove and posterior to the ventral head of the hyomandibular is a region without ossification. JARVIK (1980) suggests that the cavity in this area probably contained the saccule, and also suggests that the surface was pierced by a fenestra ovalis. The surface of this region is ossified in *Ectosteorhachis* (ROMER, 1937), but shows no evidence of a fenestra ovalis. Without direct evidence of an opening comparable to the fenestra ovalis of tetrapods, a claim that a fenestra ovalis is present in *Eusthenopteron* is premature.

THE ANTERIOR VERTEBRAE OF *Eusthenopteron*

The anterior portion of the vertebral column of *Eusthenopteron* has been described previously by JARVIK (1975, 1980) based on serially ground sections, and by ANDREWS & WESTOLL (1970) based on disarticulated material. JARVIK's (1975) reconstruction shows a large supraneural blade over the first two neural arches, which he interpreted as the fused supraneurals of these two segments, and small supraneurals above each succeeding segment up to about segment 10 (Fig. 2A). He also reconstructs the "interdorsals" with small flanges extending up to cup the ventral surface of the neural canal, and with foramina for the dorsal and ventral roots of the

spinal nerves. In this reconstruction, ribs are present from the fifth or sixth segment back. The reconstruction by ANDREWS & WESTOLL (1970) includes no supraneurals, and the segments are spaced farther apart (Fig. 2B). There is little if any difference between the anterior and trunk vertebrae in their reconstruction. The reconstruction was made from disarticulated material (specimen BMNH P. 6796a), and the element shown as the neural arch of segment 3 (ANDREWS & WESTOLL, 1970, Fig. 20a) is likely a supraneural (pers. observ.). By preparation and direct observation of articulated material, the discrepancies between these two previous reconstructions can be resolved.

In RM 14234, vertebrae 2 through 5 are articulated and not greatly disturbed from the position they would have held in life (Fig. 3). The first neural arch is rotated horizontally so

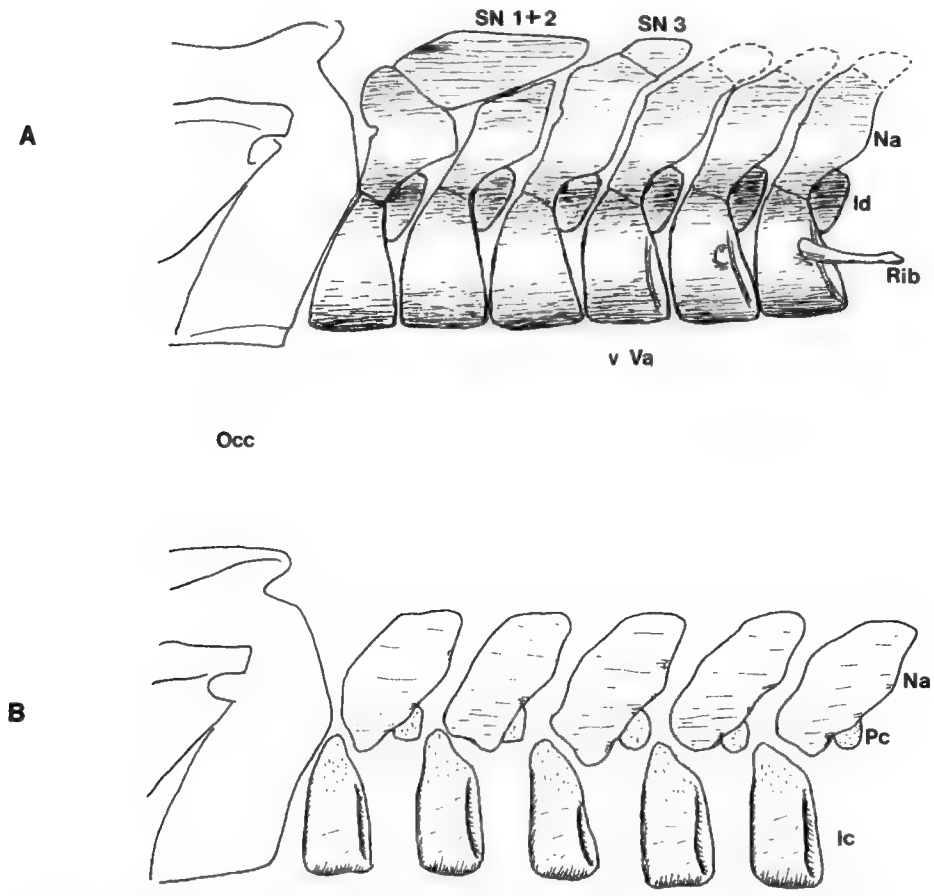

FIG. 2. — Previous reconstructions of the cranio-vertebral joint in *Eusthenopteron*. A, based on JARVIK (1975); B, based on ANDREWS & WESTOLL (1970, text and figures).

Précédentes reconstitutions de l'articulation cranio-vertébrale chez Eusthenopteron. *A, selon JARVIK (1975) ; B, selon ANDREWS & WESTOLL (1970, texte et figures).*

that the nature of its articulation with the occiput cannot be seen. The first intercentrum is also disarticulated, lying ventrolateral to intercentrum 2. There is a gap between neural arches 5 and 6, owing to arch 5 having been pushed anteriorly and arch 6 pushed posteroventrally. Intercentrum 7 is articulated with intercentrum 6; however its arch is obscured by two or three disarticulated arches that lie at the posterior margin of the block. Supraneural spines are present above the neural arches of segments 1, 3, and 5, while there are no ossified spines above arches 2 and 4, and there is no indication of a neural or supraneural ossification above arch 6.

All the intercentra appear to be paired crescents in ROM 1245. In BMNH P. 6796a and GN 790, some of the intercentra are fused, producing horseshoe-shaped unitary intercentra. This does not seem to be size related. GN 790 has intercentra 9 mm in diameter and BMNH P. 6796a has intercentra 18 mm in diameter, while ROM 1245 has intercentra roughly 20 mm or more in diameter but shows no fusion (these centra are splayed, so that the diameter is estimated). All the intercentra visible in ROM 1245 and RM 14234 have a vertical ridge of unfinished bone on the lateral face, and immediately posterior to this a vertical groove for the intersegmental artery (Fig. 4). The whole external surface of the posterior half of the centrum is of periosteal bone, except for the ridge which was probably continuous with the myoseptum. Anterior to the ridge there is some periosteal bone missing, particularly in the dorsal half. This differs from the description by ANDREWS & WESTOLL (1970) in which the dorsal half of the entire centrum was described as being devoid of periosteal cover. The ventral surface of the intercentrum is flattened and smooth, with neither the ridge nor groove extending to this region. In life the two halves of the intercentrum would have abutted ventrally such that the flattened ventral regions would

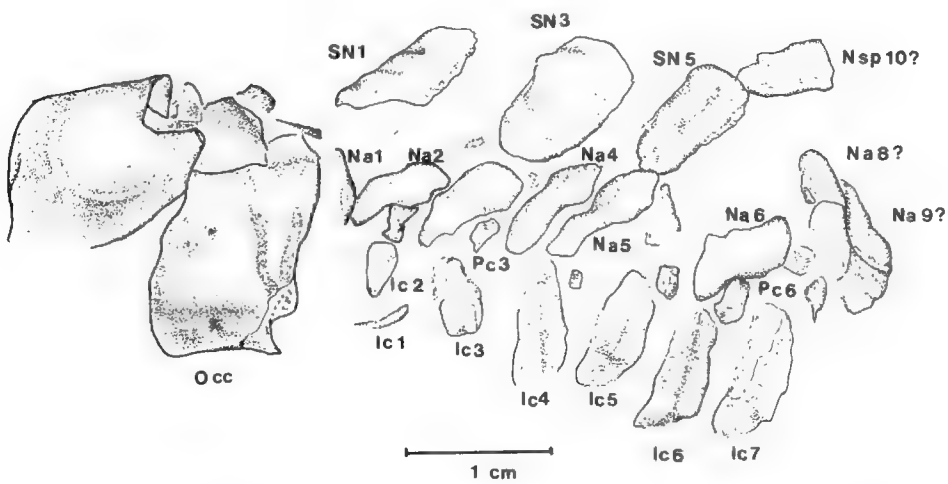

FIG. 3. — The articulated anterior portion of the vertebral column of *Eusthenopteron* exposed by preparation of specimen RM 14234. Note that the exposed surface is not flat, so that some of the elements appear distorted. For details of individual elements, see figures 4 to 6.

*Portion articulée de la colonne vertébrale d'*Eusthenopteron *révélée par la préparation du spécimen RM 14234. Noter que la surface exposée n'est pas plate, de sorte que quelques-uns des éléments apparaissent comme déformés. Pour le détail de chaque élément, voir les figures 4 à 6.*

FIG. 4. — The intercentra of specimen RM 14234.
Intercentres du spécimen RM 14234.

form a channel, concave ventrally, for the dorsal aorta (ANDREWS & WESTOLL, 1970; JARVIK, 1980). The dorsal end of the lateral face, which underlies the neural arch, bears a slight depression. Neither the ridge nor groove extend to this region. There is no evidence of sutural contact between intercentrum and arch. None of the first seven intercentra show evidence of parapophyses or ribs. The first and second intercentra in RM 14234 appear to be narrower and less robust than in succeeding segments. This may be due to preservation, since in ROM 1245 all exposed intercentra appear to be equally robust.

The neural arches are small and closely spaced. Arches 2 through 6 are similar in shape (Fig. 5), while arch 1 is rotated 90 degrees so that its posterior margin is obscured by arch 2, and its complete outline cannot be seen. The ventral portion of each arch that overlaps the intercentrum is more vertical when viewed laterally, and more oblique when viewed anteriorly or posteriorly. The dorsal portion, which covers the spinal cord, is angled posterodorsally when viewed laterally, but appears more vertical than the ventral half when viewed in anterior or posterior aspect. The lateral surface is smooth as is seen in more posterior arches and spines, with no striations or muscle scars, except for a longitudinal boss on the ventrolateral margin of arch 1. Because of the orientation of the dorsal portion of the arches, they lie close to one another, with the dorsal half of one arch extending over the ventral half of the following arch, although there are no articulating facets. These incipient zygapophyses occur lateral or ventrolateral to the spinal cord and are paired, whereas in most trunk and caudal segments incipient zygapophyses occur dorsal to the nerve cord on the neural spines, and are median.

In RM 14234, the pleurocentra (interdorsals of JARVIK) present between the ventral halves of successive neural arches are small and poorly preserved, and as such it is difficult to ascertain their exact shape (Fig. 5). They are higher than wide, with a convex lateral surface of fragile periosteal bone. There is no evidence of nerve canals, and their position between the ventral halves of successive arches below the incipient zygapophyses and adjacent to the dorsal extremity

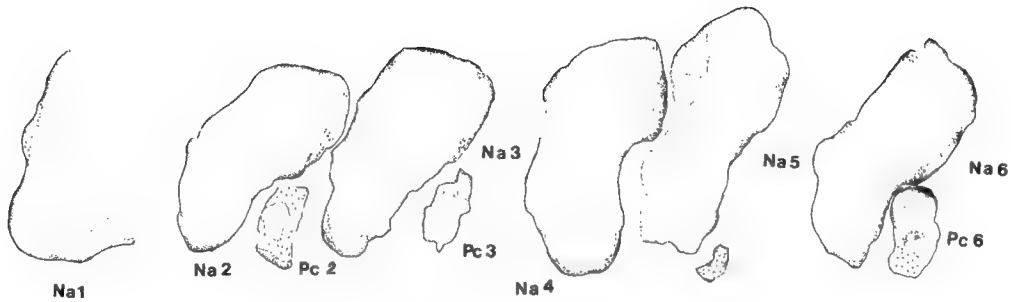

FIG. 5. — The pleurocentra and neural arches of RM 14234.
Pleurocentres et arcs neuraux de RM 14234.

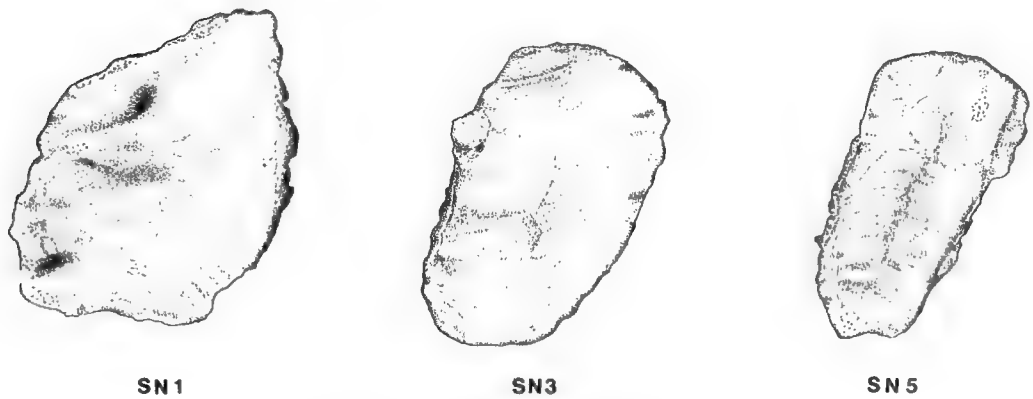

FIG. 6. — The supraneurals of RM 14234.
Supraneuraux de RM 14234.

of the intercentrum implies a position on the dorsolateral surface of the notochord, rather than lateral to the spinal cord.

The supraneural spines in RM 14234 are larger than any previously described for *Eusthenopteron foordi* (Figs. 3, 6, 7). Supraneurals are present above arches 1, 3 and 5. There is insufficient space between successive supraneurals to accommodate supraneurals above arch 2 or 4. Each is broad and lies in line with the dorsal portion of the arch with which it is associated. The lateral surface of each is marked with distinct longitudinal striations, and the anterior and posterior margins bear thin flanges and grooves. The ventral margins are rounded, showing no evidence of articulation with the arches. They are at least as thick as the neural spines of the trunk segments, and are probably of cancellous bone, as indicated by the fact that supraneural 5 has been crushed in the middle, but suffered little deformation around the periphery. The spines are unpaired median elements.

Supraneural 1 has been deformed anterodorsally, but is roughly ogival in outline with a flattened ventral margin (Fig. 6) and is the broadest of the supraneurals. The anterior margin is rough and uneven, with a thin median flange which was presumably continuous with the dorsal median septum. Three deep grooves run to the anterior margin, one ventrally and two dorsally. The dorsal grooves are separated by a ridge, and extend for almost one third of the width of

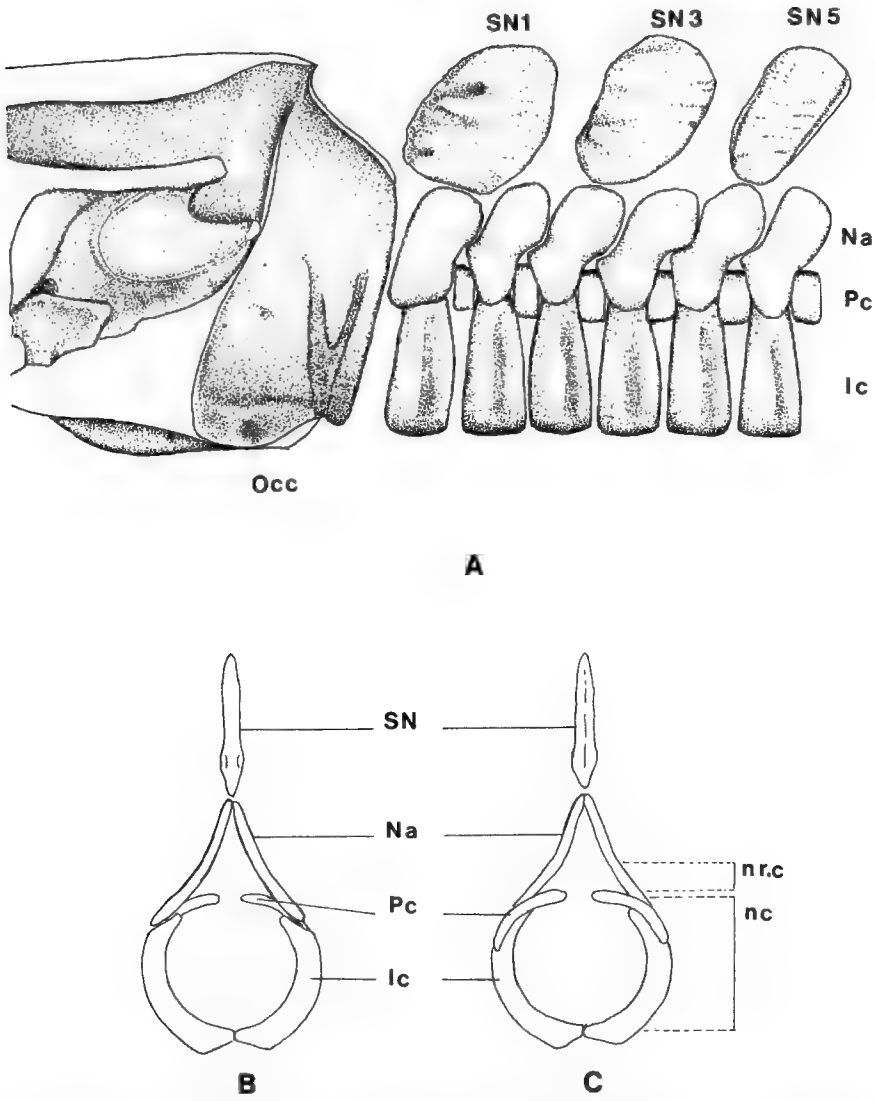

FIG. 7. — A reconstruction of the anteriormost vertebrae and occiput of specimen RM 14234. A, left lateral view; B, anterior view; C, posterior view. (From HITCHCOCK, 1992, Fig. 13).

Reconstitution des vertèbres les plus antérieures et de l'occiput du spécimen RM 14234. A, vue latérale gauche ; B, vue antérieure ; C, vue postérieure. (D'après HITCHCOCK, 1992, fig. 13).

the bone. The lateral surface is covered by tiny striations, mostly longitudinally, but some slightly oblique.

Supraneural 3 is also oval, but narrower than SN 1 (Fig. 6). It bears longitudinal striations and one deep groove across the dorsal tip. The anterior face bears a groove along its middle third, bordered top and bottom by raised processes, which are extensions of lateral ridges. The posterior margin of this element is not marked by a median flange. Supraneural 5 is narrower than both SN 1 and 3, being almost rectangular in shape with the dorsal end slightly wider than the ventral end. The striations are less distinct, and this element is more crushed than the others. A distinct median flange lies along the posterior margin, while a short groove is visible in the upper part of the lower half of the anterior margin.

A portion of a spine, broken transversely, lies dorsal to the column at the posterior margin of the specimen. Unlike the first three supraneurals it is not crushed, and its surface is smoother, although it still bears striations and a small process. Unlike a neural arch, it bears a periosteal covering and is convex on both sides. It is uncertain whether it is a supraneural for segment 6 or 7, or if it is the dorsal half of a more posterior neural spine. The latter seems more likely, owing to the texture of the bone and its resemblance to more posterior spines of other specimens.

DISCUSSION

Development of supraneurals

Ossified elements dorsal to the neural arches are common in fishes. Embryologically these elements may either grow upward from the neural arches as neural spines, or down towards the neural arches as derivatives of fin radials (Goodrich, 1930). In fossil fishes these elements may be fully formed in cartilage before becoming ossified, obscuring the direction of growth and confounding their developmental origins.

Eusthenopteron has long blade-like neural spines on trunk and tail segments. Rod-like dorsal fin radials are found only in association with the fins: one proximal radial with the first dorsal fin, two with the second dorsal fin (one of which is fused with the middle radials), and fused to the neural spines in the caudal fin. This suggests that the supraneurals were derived most probably from the neural spines.

Elsewhere in the vertebral column of *Eusthenopteron* there is ossification at the junction of the myoseptum and dorsal median septum immediately dorsal to the neural arches. No such ossification is present dorsal to neural arches 2, 4 and 6, which indicates that the myotomes may have been fused, at least medially, and that the myoseptum did not intersect the median septum in these places, but this cannot be proven.

Variation within the vertebral column of *Eusthenopteron*

The anteriormost segments of the vertebral column differ from the more posterior trunk and tail regions in *Eusthenopteron*. The trunk and tail segments have long neural and haemal spines projecting posterodorsally and posteroventrally, respectively, spanning several succeeding segments (Fig. 8B, C). In the trunk and tail of fishes, the myotomes of the right and left sides

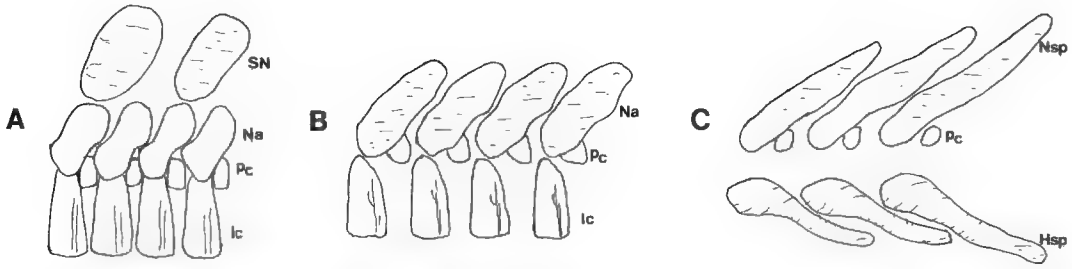

FIG. 8. — Regional variation in the vertebral column of *Eusthenopteron*. A, anterior, segments 3 to 6; B, mid trunk, approximately segments 20 to 23; C, posterior trunk, approximately segments 40 to 42. B and C based partly on ANDREWS & WESTOLL (1970).

Variations de la morphologie de la colonne vertébrale selon les régions du corps chez Eusthenopteron. *A, partie antérieure, segments 3 à 6 ; B, partie moyenne du tronc, approximativement segments 20 à 23 ; C, partie postérieure du tronc, approximativement segments 40 à 42. B et C fondées en partie sur* ANDREWS & WESTOLL *(1970).*

contract alternately to produce a strong oscillation at the tail for locomotion. The neural and haemal spines act to limit the lateral flexibility of the trunk during locomotion so that the force can be maximized at the tail (HILDEBRAND, 1988). This pattern does not absolutely restrict lateral flexion but allows for lateral flexibility of the body if the muscles of only one side are contracted.

The myotomes in the region between the skull and the pectoral girdle are not used primarily for locomotion (JARVIK, 1980) but for respiration and feeding. The epaxial musculature has a large area of insertion on the posterior and lateral faces of the braincase in *Amia* (JARVIK, 1980) and *Latimeria* (MILLOT & ANTHONY, 1958) and probably in *Eusthenopteron* as well judging by the deep fossa bridgei. For raising the skull or for ventilation of the gills, the muscles in this region act bilaterally, rather than alternately, so that both opercula are opened simultaneously, or in raising the head both sides of the back of the skull are pulled back simultaneously.

This explains why the morphology of the anteriormost vertebral elements differs from that of more posterior segments. Instead of acting to resist lateral flexion of the vertebral column, the spines in this region act to bridge the myotomes of the two sides with a solid connection. Bilateral contraction of the epaxial musculature would act to pull back the top of the skull, and raise the snout. The close proximity of the neural spines in more posterior segments severely restricts vertical flexion of the vertebral column. In the anterior region of the vertebral column, the lack of ossified elements above arches 2 and 4 allows the supraneurals of segments 1, 3 and 5 to be pulled closer together to allow dorsal flexion. The decoupling of neural arches and supraneurals allows the supraneurals to move independently of the arches. Thus the rapid movement of the supraneurals during a powerful contraction of the epaxial muscles would not place great stress on the spinal cord.

SKULL KINETICS AND FEEDING MECHANICS

The function and degree of kinetism of the skull in *Eusthenopteron* and other osteolepiforms remains a controversial issue. It is believed by many paleontologists (WATSON, 1926; ROMER, 1937; THOMSON, 1967; 1969) that significant movement was possible between ethmosphenoid

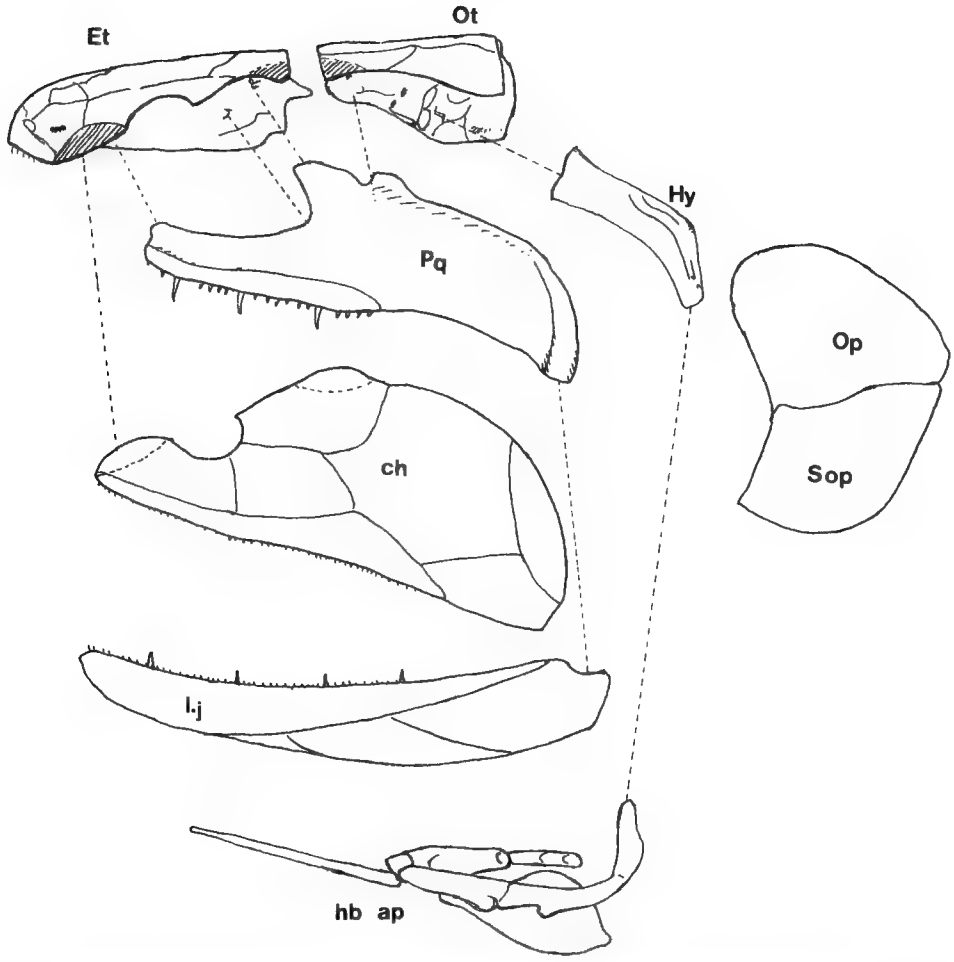

FIG. 9. — The separate skeletal units that comprise the head of *Eusthenopteron*. The hatched areas on the snout and skull roof indicate the region of overlap by the cheek plate. (From HITCHCOCK, 1992, Fig. 1; based in part on JARVIK, 1980, Figs. 107, 110, 112).

Les différentes unités squelettiques comprises dans la tête d' Eusthenopteron. *Les zones hachurées sur le museau et le toit crânien indiquent la zone de recouvrement par la plaque de la joue. (D'après HITCHCOCK, 1992, fig. 1. (en partie d'après JARVIK, 1980, figs 107, 110, 112).*

and otoccipital portions of the braincase, while others (JARVIK, 1954; 1980; BJERRING, 1971; 1978) believe that kinetism is impossible if the interconnections between all the components are considered.

The following examination of the components of the head (Fig. 9), starting from the hypobranchial apparatus and working up, describes the mobility of which the skull was likely capable. The ceratohyals of the hypobranchial apparatus are braced against the inner surface of

the lower jaw. The principal function of this apparatus is the ventral expansion of the oralobranchial cavity. Such an expansion is produced by contraction of the sternohyoideus muscle pulling the basket posteriorly. This also generates a strong lateral force on the posterior extremity of the jaws, as in modern bony fish (ALEXANDER, 1970). The loose symphysial connection of the lower jaws implies that the angle between them was not fixed. If the posterior end of the lower jaws moved laterally, the quadrate must follow or the jaws would disarticulate. There must therefore be some degree of lateral movement of the palatoquadrate with respect to the endocranium. The articulation of the palatoquadrate to the otical shelf lies in line with the articulation of the processus connectens and would not prevent movement of the intracranial joint. THOMSON (1967) states that the palatoquadrate was not connected to the otical shelf, but whether this connection of the palatoquadrate exists or not is of little importance to its mobility. Also contrary to THOMSON (1967) and SMITHSON & THOMSON (1982) there appears to be no firm connection between the hyomandibular and the palatoquadrate.

If the palatoquadrate hinges laterally then there must also be some flexibility of the cheek, because the ectopterygoid abuts the medial surface of the maxilla. The small areas where the cheek overlaps the skull roof and snout likely allowed some sliding and would not prevent the cheek from moving laterally. The sliding nature of the overlap of the postorbital bone of the cheek plate across the hinge line would also not prevent mobility of the intracranial joint. The processes of the supratemporal (intertemporal of JARVIK) extending below the hinge line would limit, but not prevent skull kinesis. Muscle scars on the ventral surface of the braincase indicate the presence of a large subcephalic (or basicranial) muscle mass, which in the living *Latimeria* is responsible for flexion of the intracranial joint (MILLOT & ANTHONY, 1958).

The feeding mechanism in *Eusthenopteron* (Fig. 10) was probably much like that proposed for *Latimeria* by LAUDER (1980), which differs from the interpretation by THOMSON (1967). The initial action in the feeding mechanism of *Eusthenopteron* was the contraction of the anterior epaxial muscles to raise the skull. The result of this was not only to raise the upper jaws, but also to depress the lower jaws. Contraction of the strong anterior epaxial muscles resulted in the posterodorsal rotation of the endocranium, which pivoted around a point posterior to the occiput, at the dorsal margin of the notochord. The palatoquadrate, which is attached to the endocranium at several points, rotated with it, thrusting the quadrate joint forward. In this initial phase of jaw opening, as the endocranium is swung upward, the quadrate joint is swung like a pendulum through an arc from a point below and behind the occiput to a point below and in front. The effective lever has the dorsal part of the occiput as the short arm, the occipital-vertebral joint as the fulcrum, and the quadrate articulation as the distal point of the long arm. The motion of the sort arm (dorsal part of occiput) is magnified in the long arm (quadrate) by a factor of about twelve to one.

The lower jaw is a lever with the short arm between the quadrate articulation and the lateral process of the ceratohyal. The long arm is from this articulation to the symphysis, and is about five times as long as the short arm. The fulcrum is below and in front of the articular so that the rotation of the mandible is in the opposite direction to that of the palatoquadrate. The motion of the skull is magnified in the motion of the quadrate and is magnified again in the swing of the symphysis. Thus the short powerful contraction of the epaxial muscles not only raises the skull and upper jaws, but is also responsible for the rapid lowering of the mandibles.

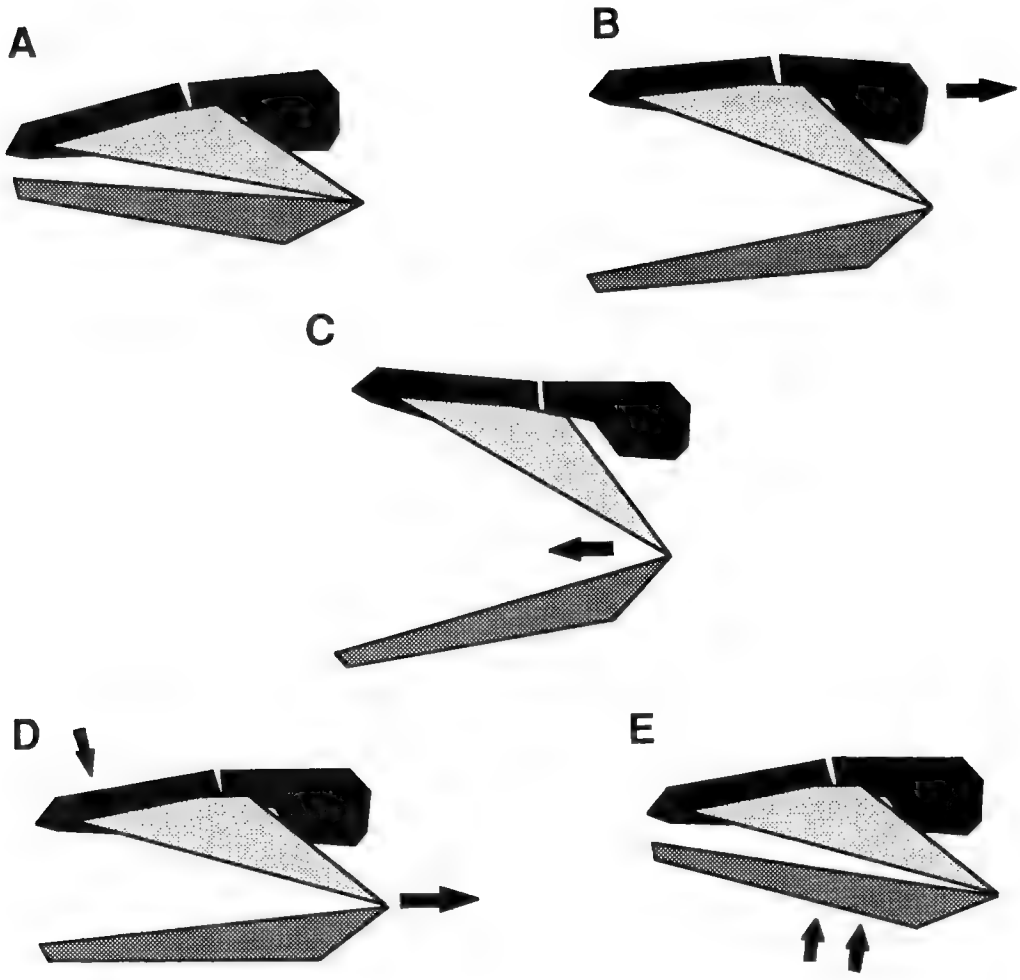

FIG. 10. — The feeding mechanism of *Eusthenopteron*. A, from the resting position, the epaxial musculature inserting in the fossa bridgei contracts, pulling the skull up and back (B); C, the notochord compresses slightly, then releases the stored energy, hyperextending the ethmosphenoid. This snaps the quadrate forward, rotating the lower jaw around the articulation with ceratohyal 1; D, initiation of jaw closure is through contraction of the subcephalic muscles, which swings the quadrate posteriorly, rotating the lower jaw into position for final jaw closure through contraction of the adductor muscles (E).

Mécanisme de la manducation chez Eusthenopteron. *A, à partir de la position de repos, la musculature épaxiale qui s'insère dans la fosse de Bridge se contracte, tirant le crâne vers le haut et vers l'arrière (B) ; C, la notochorde se comprime légèrement, puis relâche l'énergie emmagasinée en mettant l'ethmosphénoïde en forte extension. Cela a pour effet de propulser le carré vers l'avant, faisant pivoter la mandibule autour de l'articulation avec le cératohyal 1 ; D, le déclenchement de la fermeture de la bouche se fait par contraction des muscles subcéphaliques, qui projettent le carré vers l'arrière, faisant ainsi pivoter la mandibule dans sa position finale de fermeture des mâchoires par contraction des muscles adducteurs (E).*

Since the skull is raised as a unit, there is no need for a large muscle mass to raise the ethmosphenoid with respect to the otoccipital, and indeed none has been found (MILLOT & ANTHONY, 1958; THOMSON, 1967; JARVIK, 1980). The ethmosphenoid may be slow in raising, because of some compressibility of the notochord, but this compressibility may have played a part in jaw opening and closing. The notochord may have acted as an elastic element in the intracranial joint, so that as the otoccipital is pulled back and up, rotation of the ethmosphenoid is delayed by its inertia and the energy is stored in the notochord like a compressed spring. When the otoccipital is extended maximally, the notochord spring releases its energy and the ethmosphenoid snaps up and becomes hyperextended, further increasing the swing of the quadrate. The stretched notochord would then help in the downward acceleration of the ethmosphenoid during the initial phase of jaw closure.

If the lower jaw is depressed by a forward swing of the quadrate, then initiation of jaw closure may be by way of a rearward swing of the quadrate. Such a swing may be induced by means of the subcephalic (or basicranial) muscles. Contraction of these muscles produces a rotation of the ethmosphenoid and palatoquadrate around the processus connectens, and the quadrate is thrust posteriorly, swinging the lower jaw in the reverse of the manner of opening, without having to overcome the inertia of the entire skull. The fulcrum this time is the intracranial joint. The long lever arm is longer than in the opening sequence, and the short lever arm is the effective position of the subcephalic muscles. The fulcrum of the mandible initially is the area of insertion of the anteriormost (deep) portion of the adductor mandibulae, which has the most posteriorly directed fibres (THOMSON, 1967; JARVIK, 1980). Because the intracranial joint is located more anterior than the occiput, the swing of the quadrate has a greater vertical component than in initial phase of the opening sequence, so that in the later stage of its swing both the quadrate and the adductors act to lift the mandible. In this way a slight flexure of the intracranial joint has a large effect on the gape. Final jaw closure is by contraction of the posterior (lateral) portions of the adductor mandibulae, which pull the jaw up against the skull.

This model is also in agreement with LUND *et al.* (1985), who claim that the crushing aspect of ethmosphenoid flexion, i.e. THOMSON's (1967) model of rhipidistians and LAUDER's (1980) model of *Latimeria*, in which ethmosphenoid contraction is the last phase of jaw closure and is used to puncture prey, has been exaggerated, particularly when it concerns coelacanths with feeble dentition.

Simultaneous ventral and lateral expansions of the hypobranchial apparatus and cheeks increase the volume of the oralobranchial cavity. This also forces the stylohyal laterally, and in conjunction with the protraction of the hyomandibular the operculars are forced open. All of these actions help to produce suction to aid prey capture. This may well continue late in the cycle to compensate for the volume reduction caused by closing the jaws, as in *Amia* (LAUDER, 1979). Use of the subcephalic muscles to initiate jaw closure does not draw the palatoquadrate complex medially, while muscular action directly on the palatoquadrate would. This would help prevent the oralobranchial cavity from becoming prematurely reduced in volume during jaw closure.

CONCLUSION

The anterior portion of the vertebral column in *Eusthenopteron* possesses large blade-like supraneural spines separate from the neural arches, above arches 1, 3, and 5. The supraneurals act to bridge the epaxial myotomes of the right and left sides, and are positioned to allow rapid and powerful contraction of these muscles. The contraction of these muscles pulls the skull back, raising the snout and swinging the quadrate forward. This forward swing of the quadrate combined with the posteroventral motion of the hypobranchial apparatus acts to rotate the lower jaws downward. The final stage of jaw opening involves the hyperextension of the ethmosphenoid, further increasing the gape. Initiation of jaw closure may be through contraction of the subcephalic muscles, in the reverse of the final stage of jaw opening. Jaw closure is completed by contraction of the adductor muscles, pulling the lower jaws up against the skull. In this model there is a greater swing of the quadrate than in previous models, due to a greater participation of the otoccipital, and the fact that the hyomandibular is not firmly connected to the palatoquadrate. This model also places a greater emphasis on the suction aspect of the feeding mechanism of *Eusthenopteron*, and less on the biting aspect of previous models.

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Morphology of a new osteolepidid fish from Russia

by Oleg A. LEBEDEV

Abstract. — The morphology of a new Devonian osteolepidid fish, *Medoevia lata* n. g., n. sp. is described. The specimen originates from an unknown locality, and dating was made on the basis of a tooth of *Phoebodus australiensis* Long, morphotype 1 (GINTER, 1990), found during the chemical preparation. This suggests an age ranging from the lower *P. trachytera* to the *Siphonodella praesulcata* conodont zones (Upper Famennian). A slightly younger age is suggested by the discovery of scales identical to those of *Medoevia* in the Late Tournaisian of Belarus. The perfect three-dimensional state of preservation allows the study of the dermal skeleton of the skull, the neurocranium, visceral arches and the postcranial skeleton of the anterior part of the trunk. The new form is characterized by the connection of hypobranchial 4 to hypobranchial 3, a condition known elsewhere in the porolepiform *Glyptolepis groenlandica* Jarvik, and by generally cycloid scales with a median boss on the inner surface, combined with a cosmine-covered external surface. The crista parotica is directed backwards and supports both the tabular and the extratemporal along the suture between them. No apomorphic feature is found at present for the Osteolepididae and the group may be considered to be paraphyletic with respect to the Eusthenopteridae, Rhizodopsidae, Canowindridae, Megalichthyidae and Lamprotolepididae.

Keywords. — Vertebrata, Osteolepiformes, Late Devonian, Russia, anatomy, phylogeny.

Morphologie d'un nouvel Osteolepididae de Russie

Résumé. — La morphologie d'un nouveau poisson Ostéolépididé, *Medoevia lata* n. g., n. sp. est décrite. Le spécimen provient d'une localité inconnue, et sa datation a été effectuée sur la base d'une dent de *Phoebodus australiensis* Long, morphotype 1 (GINTER, 1990), trouvée lors de la préparation chimique du spécimen. Cela suggère un âge allant de la zone de Conodontes à *Palmatolepis trachytera* inférieure à la zone à *Siphonodella praesulcata* (Famennien supérieur). Un âge légèrement plus récent peut aussi être avancé sur la base de la découverte d'écailles identiques à celles de *Medoevia* dans le Tournaisien supérieur de Belarus. L'état de conservation parfait et tridimentionnel du spécimen a permis l'étude du squelette dermique du crâne, du neurocrâne, des arcs viscéraux et du squelette postcrânien de la partie antérieure du tronc. Cette nouvelle forme diffère des autres Ostéolépididés par le contact entre les hypobranchiaux 4 et 3, caractère connu ailleurs chez le Porolépiforme *Glyptolepis groenlandica* Jarvik, ainsi que par des écailles cycloïdes pourvues d'une bosse médiane sur leur face interne. La crista parotica est dirigée postérieurement et soutient à la fois le tabulaire et l'extratemporal, le long de leur suture commune. Aucun caractère apomorphe ne peut être défini pour les Ostéolépididés, qui peuvent donc être considérés comme paraphylétiques par rapport aux Eusthenoptéridés, Rhizodontidés, Canowindridés, Mégalichthyidés et Lamprotolépididés.

Mots-clés. — Vertebrata, Ostéolépiformes, Dévonien supérieur, Russie, anatomie, phylogénie.

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INTRODUCTION

The study of the morphology of the osteolepiform fishes is perhaps one of the most thoroughly explored fields in vertebrate palaeontology but, in contrast to Eusthenopteridae, brilliantly investigated by E. JARVIK in a series of works on *Eusthenopteron foordi*, the study of the osteolepidids is much more modest, due to their usually poorer state of preservation.

The study of the endocranial structures is restricted to a few papers by FISCHER (1852), WATSON (1925, 1926, 1954), JARVIK (1942, 1966, 1980), ROMER (1937, 1941), THOMSON (1964a, b, 1965, 1966, 1967), JANVIER (1978, 1980), JANVIER & MARCOUX (1976), JANVIER *et al.* (1979), VOROBYEVA (1975, 1977a, b, 1981), VOROBYEVA & LEBEDEV (1986a), LEBEDEV (1983), LONG (1985b, 1987) and such structures as the visceral arches were previously entirely unknown.

A new three-dimensionally preserved specimen, unfortunately derived from an unknown locality, provides a possibility to answer some questions on the morphology and relationships of the osteolepidid fishes. It is noted that no unique apomorphic features are known for the moment for the Osteolepididae and the group may be regarded as paraphyletic with respect to other osteolepiform families.

The new form possesses several features which demonstrate the close relationship of the Osteolepididae with the Eusthenopteridae.

ABBREVIATIONS

aa1 gr	groove for the afferent artery of the first branchial unit, *sillon pour l'artère afférente de la première unité branchiale*;
ab	anterior buttress of the endoskeletal shoulder girdle, *arc-boutant antérieur de la ceinture scapulaire endosquelettique*;
abc ar	anterior area of the attachment surface of the basis cranii muscle on the otico-occipital block, *zone antérieure de l'aire d'insertion du muscle basicrânien sur le bloc otico-occipital;*
acf	auxillary connecting facet of the autopalatine, *facette de contact auxilliaire pour l'autopalatin*;
aci fo	foramen for the a. carotis interna, *foramen pour l'artère carotide interne*;
ad fo	adductor fossa, *fosse pour les muscles adducteurs*;
ads	adsymphyseal plate, *plaque adsymphysaire*;
ahy ri	ridge for the insertion of m. hyomandibularis, *crête pour l'insertion du muscle hyomandibulaire*;
ano	anocleithrum, *anocleithrum*;
ano pr	anocleithral process, *processus anocleithral*;
ano pr gr	groove of the cleithrum housing the anocleithral process, *sillon du cleithrum logeant le processus anocleithral;*
aom fo	foramen for the a. ophthalmica magna, *foramen pour l'artère ophthalmique principale*;
aor fo	foramen for the orbital artery, *foramen pour l'artère orbitaire*;
ap pt	apical process of the autopalatine, *processus apical de l'autopalatin*;
ar fo	foramen for the articular canal, *foramen pour le canal articulaire*;
ar ri + kn	articulation ridge and knob of scale, *crête articulaire et processus des écailles*;
asc pr	ascending process of the palatoquadrate, *processus ascendant du palatocarré*;
aup	autopalatine, *autopalatin*;
av gr	groove for the vertebral artery, *sillon pour l'artère vertébrale*;
bb1	anterior basibranchial element, *élément basibranchial antérieur*;
bb2	posterior basibranchial element, *élément basibranchial postérieur*;

bc fen	basicranial fenestra, *fenêtre basicrânienne*;
bh fo	buccohypophyseal foramen, *foramen bucco-hypophysaire*;
bp pr	basipterygoid process, *processus basiptérygoïde*;
b pr	basal process of the palatoquadrate, *processus basal du palatocarré*;
ca hu	humeral head, *tête humérale*;
ch2	cératohyal 2, *cératohyal 2*;
clav	clavicula, *clavicule*;
clav ar	articulation area of the cleithrum for the clavicle, *surface d'articulation pour la clavicule sur le cleithrum*;
clei	cleithrum, *cleithrum*;
co pi	coronoid fang pit in autopalatine, *dépression pour le croc coronoïdien dans l'autopalatin*;
crs	crista suspendens, *crista suspendens*;
da gr	groove for the dorsal aorta, *sillon pour l'aorte dorsale*;
db	dorsal buttress of the endoskeletal shoulder girdle, *arc-boutant dorsal de la ceinture scapulaire endosquelettique*;
dl ri	dorsolateral ridge, *crête dorsolatérale*;
dmax pr	dorsal maxillary process, *processus maxillaire dorsal*;
dm pr	dorsomedial process of autopalatine, *processus dorsomédial de l'autopalatin*;
dmp pi	pit for the articulation with the dorsomedial process of the palatoquadrate, *dépression pour l'articulation avec le processus dorsomédial du palatocarré*;
dm pr	dorsomedial process of the autopalatine, *processus dorsomédial de l'autopalatin*;
ea1 gr	groove for the efferent artery of the first branchial unit, *sillon pour l'artère efférente de la première unité branchiale*;
ect ri	ectepicondylar ridge, *crête ectépicondylaire*;
ent fo	entepicondylar foramen, *foramen entépicondylaire*;
epa tu	tubercle on the ventral side of the ethmoid, between the anterior processes of the parasphenoid, *tubercule sur la face ventrale de l'ethmoïde, entre le processus antérieur et le parasphénoïde*;
esl	lateral extrascapular, *extrascapulaire latéral*;
esm	median extrascapular, *extrascapulaire médian*;
et	extratemporal, *extratemporal*;
exl ar	operculum area overlapped by the lateral extrascapular, *zone de l'operculaire recouverte par l'extrascapulaire latéral*;
ex no	external nostrils, *narines externes*;
fra fo	foramen for the r. frontalis anterior of the n. profundus, *foramen pour le rameau frontal antérieur du nerf profond*;
ghy tu	tubercle on the urohyal for the origin of m. geniohyoideus, *tubercule sur l'urohyal pour l'insertion du muscle géniohyoïdien*;
gl	glenoid fossa, *fosse glénoïde*;
gla	lateral gular, *gulaire latéral*;
gl fo	glenoid foramen, *foramen glénoïdien*;

gme — median gular, *gulaire médian*;
har d — dorsal articulation area for the hyomandibula, *articulation dorsale pour l'hyomandibulaire*;
har v — ventral articulation area for the hyomandibula, *articulation ventrale pour l'hyomandibulaire*;
hb4 ar — articulation area for hypobranchial 4 on the hypobranchial 3, *surface d'articulation pour l'hypobranchial 4 sur l'hypobranchial 3*;
hu ri — humeral ridge, *crête humérale*;
hy ar — articulation facet on the opercular for the opercular process of hyomandibula, *surface articulaire sur l'operculaire pour le processus operculaire de l'hyomandibulaire*;
hyc — orifice of the hyomandibular canal, *orifice du canal hyomandibulaire*;
ial tu — tubercles for the attachment of the interarcual ligament, *tubercules pour l'attache du ligament interarcual*;
icl — interclavicle, *interclavicule*;
icl ar — overlap area for the interclavicle, *surface de recouvrement pour l'interclavicule*;
iosc fo — foramen of the infraorbital sensory canal in the postorbital, *foramen du canal sensoriel infraorbitaire dans le postorbitaire*;
ipb1 ar — articular area for the infrapharyngobranchial 1, *surface d'articulation pour l'infrapharyngobranchial 1*;
ipb2 ar — articular area for the infrapharyngobranchial 2, *surface d'articulation pour l'infrapharyngobranchial 2*;
it — intertemporal, *intertemporal*;
it ar — intertemporal contact area on the postorbital, *surface de contact pour l'intertemporal sur le postorbitaire*;
ivc — intervomerine canal, *canal intervomérin*;
ju — jugal, *jugal*;
ju gr — jugular groove, *sillon jugulaire*;
ju ri — jugular ridge, *crête jugulaire*;
juv — jugular vein groove on hyomandibular, *sillon pour la veine jugulaire sur l'hyomandibulaire*;
lc — lateral commissure, *commissure latérale*;
lj no — notch in the anterior edge of the submandibulo-branchiostegal for the lower jaw contact, *encoche dans le bord antérieur du submandibulo-branchiostège, pour le contact avec la mandibule*;
lm oar — lacrymo-maxillary overlapping area, *surface de recouvrement lacrymo-maxillaire*;
lpch2 ar — subopercular area contacting the lateral process of the ceratohyal 2, *zone du sous-operculaire en contact avec le processus latéral du cératohyal 2*;
ls pr — lateral supraorbital process of the ethmoid, *processus supraorbitaire latéral de l'ethmoïde*;
ma fa — anteromedial articulation facet of the palatoquadrate, *surface d'articulation antéromédiale du palatocarré*;

mamp	area of attachment for the posterior portion of m. adductor mandibulae, *surface d'insertion pour la portion postérieure du muscle adducteur de la mandibule*;
mbpr fac gr	groove for the medial branch of the palatal ramus of the n. facialis, *sillon pour la branche médiale du rameau palatin du nerf facial*;
mem ar	medial lamina of the cleithrum overlapped by the operculum and suboperculum, *lame médiale du cleithrum recouverte par l'opercule et le sous-opercule*;
me ri	median ridge of the interclavicle, *crête médiane de l'interclavicule*;
mgh pi	insertion pit of the m. geniohyoideus, *dépression pour l'insertion du muscle géniohyoïdien*;
mlb tu	tubercles for the attachment of the principal portion of m. levator bulbi, *tubercules pour l'insertion de la portion principale du muscle levator bulbi*;
mm	mentomandibular, *mentomandibulaire*;
moi pi	pit for the attachment of the m. obliquus inferior of the eyeball, *dépression pour l'insertion du muscle oblique inférieur de l'œil*;
mov2-3 ri	ridge for the attachment of the m. obliquus ventralis, *crête pour l'insertion du muscle oblique ventral*;
mp	metapterygoid, *métaptérygoïde*;
mrb ar	attachment area for the m. retractor bulbi, *aire d'insertion du muscle retractor bulbi*;
msc ar	attachment area for the m. subcephalicus, *aire d'insertion du muscle subcéphalique*;
mshy	pocket in the basibranchial I for the insertion of m. sternohyoideus, *poche dans le basibranchial I pour l'insertion du muscle sternohyoïdien*;
mtv2 ri	ridge for the m. transversalis ventralis, *crête pour le muscle transversal ventral*;
my ri	myoseptal ridge on the intercentrum, *crête myoseptale sur l'intercentre*;
mx	maxilla, *maxillaire*;
na ar	articulation facets for the neural arch, *facettes d'articulation pour l'arc neural*;
nbcv	orifice for the ventral branch of the nasobasal canal, *orifice de la branche ventrale du canal nasobasal*;
nsp	neural spine, *épine neurale*;
oa gr	groove for the occipital artery, *sillon pour l'artère occipitale*;
oem no	notch for the oblique eye muscles, *encoche pour le muscle oblique de l'œil*;
ol fo	orifice for the r. ophtalmicus lateralis, *orifice pour le rameau ophthalmique du nerf latéral*;
ol ri	olfactory ridge, *crête olfactive*;
onc n	notch for the passage of the orbitonasal canal, *échancrure pour le passage du canal orbitonasal*;
op	operculum, *operculaire*;
op ar	opercular articulation area of the hyomandibula, *articulation operculaire de l'hyomandibulaire*;
op pr	opercular processes of the post-temporal and supracleithrum, *processus operculaires du post-temporal et supracleithrum*;

pa	parasphenoid, *parasphénoïde*;
pano pr ar	area on the cleithrum for the overlap with the posterior process of the anocleithrum, *surface du cleithrum pour le recouvrement par le processus postérieur de l'anocleithrum*;
Pa o	pores of the Paul's organ, *pores de l'organe de Paul*;
pa pi	anterior parasphenoid pit, *dépression antérieure du parasphénoïde*;
pb	posterior buttress of the endoskeletal shoulder girdle, *arc-boutant postérieur de la ceinture scapulaire endosquelettique*;
pbc ar	posterior area of the attachment surface for the m. basis cranii on the otico-occipital block, *région postérieure de la surface d'insertion du muscle basicrânien sur le bloc otico-occipital*;
pca gr	postchoanal anastomosis, *anastomose postchoanale*;
pe ri	pectoral ridge, *crête pectorale*;
pi	pineal foramen, *foramen pinéal*;
pnc	palato-nasal canal, *canal palato-nasal*;
pn pi	prenasal pit, *dépression prénasale*;
pnw	postnasal wall, *cloison postnasale*;
po	postorbital, *postorbitaire*;
po ar	intertemporal process for the postorbital overlap, *processus de l'intertemporal pour le recouvrement postorbitaire*;
pot pr	postotic process, *processus postotique*;
ppal fo	foramen for the posterior palato-nasal canal, *foramen du canal palato-nasal postérieur*;
pra pr	anterior process of the prearticular, *processus antérieur du préarticulaire*;
pr con	processus connectens, *processus connectens*;
pr fo	foramen for the n. profundus, *foramen pour le nerf profond*;
pr hy	pocket for the insertion of the m. protractor hyomandibularis, *recessus pour l'insertion du muscle protracteur de l'hyomandibulaire*;
pt	post-temporal, *post-temporal*;
ptf	post-temporal fossa, *fosse post-temporale*;
pt pr	paratemporal process, *processus paratemporal*;
qu	quadratum, *carré*;
qj	quadratojugal, *quadrato-jugal*;
rece	attachment area of the m. rectus cervicis on the urohyal, *surface d'insertion du muscle rectus cervicis sur l'urohyal*;
rhy gr	groove for the r. hyoideus, *sillon pour le rameau hyoïdien*;
rol fo	foramen for the r. ophtalmicus lateralis, *foramen pour le rameau ophthalmique du nerf latéral*;
rotl fo	foramen for the r. oticus lateralis, *foramen pour le rameau otique du nerf latéral*;
roVII fo	foramen for the r. opercularis VII, *foramen pour le rameau operculaire du nerf VII*;
rpa fo	foramen for the r. palatinus, *foramen pour le rameau palatin*;
sa fo	foramen of the suprangular canal, *foramen du canal surpra-angulaire*;

scl supracleithrum, *supracleithrum*;
sco fo supracoracoid foramen, *foramen supracoracoïdien*;
sc pro anocleithrum process for the supracleithrum overlap, *processus de l'anocleithrum pour le recouvrement du supracleithrum*;
sgl fo supraglenoid foramen, *foramen supraglénoïdien*;
sh re spiraculo-hyomandibular recess, *récessus spiraculo-hyomandibulaire*;
smb submandibulo-branchiostegal, *submandibulo-branchiostège*;
smb f ventral facet of the ceratohyal 1 contacting the submandibulo-branchiostegal, *facette ventrale du cératohyal I en contact avec le submandibulo-branchiostège*;
so 1 suborbital ledge, *rebord sous-orbitaire*;
so1 anterior supraorbital, *supraorbitaire antérieur*;
so2 posterior supraorbital, *supraorbitaire postérieur*;
so2 ar intertemporal process for the supraorbital 2 overlap, *processus de l'intertemporal pour le recouvrement du supraorbitaire 2*;
sop suboperculum, *sous-operculaire*;
sop f lateral facet of the ceratohyal 1 contacting the suboperculum, *facette latérale du cératohyal I en contact avec le sous-operculaire*;
spb1 ar articulation knob for the suprapharyngobranchial 1, *tubercule d'articulation pour le suprapharyngobranchial 1*;
spcpo fo posterior foramen of the spiracular canal, *foramen postérieur du canal spiraculaire*;
spcpod + ro fo foramen for the posterior diverticle of the spiracular canal and the r. oticus, *foramen pour le diverticule postérieur du canal spiraculaire et le rameau otique du nerf latéral*;
sq squamosal, *squamosal*;
sr sublingual rod, *tige sublinguale*;
ssc fo subscapular fossa, *fosse subscapulaire*;
stl fo foramen for the r. supratemporalis lateralis, *foramen pour le rameau supratemporal du nerf latéral*;
stl gr groove for the r. supratemporalis lateralis, *sillon pour le rameau supratemporal du nerf latéral*;
sty ar articulation facet for the stylohyal on the hyomandibula, *facette d'articulation pour le stylohyal sur l'hyomandibulaire*;
su + de ri supinator and deltoid ridges, *crêtes supinatrice et deltoïde*;
sup tu suprapterygoid articulation tubercle, *tubercule pour l'articulation supraptérygoïde*;
tp rb tu tubercle for the attachment of the transverse portion of m. retractor bulbi, *tubercule pour l'insertion de la portion transversale du muscle retractor bulbi*;
tri no trigeminal notch, *encoche trigéminale*;
uh ar area on the basibranchial 1 for the attachment of the urohyal, *surface de contact entre le basibranchial 1 et l'urohyal*;
val pr anterolateral process of the vomer, *processus antérolatéral du vomer*;

vam pr	anteromedial process of the vomer, *processus antéromédial du vomer;*
vca fo	foramen for the v. cerebralis anterior, *foramen pour la veine cérébrale antérieure*;
v font	vestibular fontanelle, *fontanelle vestibulaire*;
vo	vomer, *vomer*;
vo de	depression for the vomer in the ventral side of the ethmoid, *dépression pour le vomer dans la paroi ventrale de l'ethmoïde*;
vpit fo	foramen for the pituitary vein, *foramen pour la veine pituitaire*;
vvl	vertical lamina of the vomer, *lame verticale du vomer*;
3-7	submandibular plates, *plaques submandibulaires*;
II-XII	cranial nerve foramina, *foramens pour les nerfs crâniens II-XII.*

MATERIALS AND METHODS

The specimen described here was kindly donated to the author by Pr Georgy Ts. MEDOYEV, Polytechnical Institute, Alma-Ata, Kazakhstan. It comes from an unknown locality and no information on its age and place of origin is available. The preparation of the specimen has yielded a tooth of *Phoebodus australiensis* Long (morphotype 1, GINTER, 1990), which suggests an age interval ranging from the lower *Palmatolepis trachytera* to the *Siphonodella praesulcata* (Upper Devonian, Upper Famennian) conodont zones.

Alternating dating information originates from subsurface deposits of Belrus (borehole 326, depth 322.0, specimen 14b) that yielded fragmented scales of the same peculiar appearance as in *Medoevia* (see description of scale below). The deposits were dated as Lower Tournaisian (Upinian) by ostracods (V. I. AKHIMOVICH, V. K. GOLUBTSOV, pers. commun. 1994). The specimen of *Medoevia* described here may thus also be Lower Tournaisian in age.

The specimen was a yellowish-grey marl nodule, which contained a three-dimensionally preserved skull, but slightly compressed from the sides. The posterior part of the skull was damaged by transverse cracks filled with calcite cementation, that resulted in the disintegration of some bones in this region; most of the branchial arches were damaged.

Preparation was carried out by 10% solution of acetic acid, the remaining clay being removed with a mounted needle. The material is represented by an almost complete skull, shoulder girdle, humerus, vertebrae and anterior squamation. After preparation the specimen was separated into individual bones.

The material is kept in the Paleontological Institute, Academy of Sciences of Russia, Moscow, specimen number PIN 4482/1.

SYSTEMATIC PALEONTOLOGY

Order OSTEOLEPIFORMES Berg, 1937

Family OSTEOLEPIDIDAE Cope, 1889

Genus **MEDOEVIA** n. g.

TYPE SPECIES. — *Medoevia lata* n. sp.

ETYMOLOGY. — Named after Pr George Ts. MEDOYEV, who kindly donated the specimen to the author.

DIAGNOSIS. — An osteolepidid fish with a skull length of about 90 mm and estimated body length of about 45-50 cm. The anterior and lateral surfaces of the snout are almost vertical, with external narial openings visible from above. The ethmosphenoid-otico-occipital length ratio (b/a) is 1.22. The ethmoid-ethmosphenoid length ratio (r/b) is 0.44. The preorbital length is to the orbital + postorbital divisions together as 0.56. The pineal foramen is situated in the middle of the orbital region and opposite the anterior ends of the parietal pit-lines. The postpinealethmosphenoid shield length ratio is 0.28. The parietal pit-lines are widely displaced from the median suture, laterally. The anterior end of the parasphenoid is bifid. The otic capsules are shifted posterolaterally, hence the trapezoidal shape of the otico-occipital shield. The trigeminal notch is situated at the level of the intracranial gap. The cheek plate is 1.5 times longer than the otico-occipital shield. The maximum depth of the maxilla is 0.20 of its length. The length of the lateral gular is 2.5 times more than its width, the pit-line being situated in the anterior third of the bone. Hypobranchial 4 articulates with hypobranchial 3. The scales are predominantly cycloid, with a median internal boss and a cosmine-covered external surface.

Medoevia lata n. sp.

DIAGNOSIS. — As for the genus.

HOLOTYPE. — PIN 2879/5. The anterior part of an individual, including the skull, shoulder girdle, humerus, vertebrae and scattered scales.

TYPE HORIZON AND LOCALITY. — Unknown, probably Upper Devonian.

ETYMOLOGY. — From *latus* (Latin): broad.

DESCRIPTION

The head is rather flattened and broad. The length of the skull is about 1.5 times its maximum width. The cosmine covers all the dermal bones of the skull and shoulder girdle, except the interclavicle, clavicles and part of the cleithra (Fig. 1A-D).

DERMAL BONES OF THE ETHMOSPHENOID (FRONTO-ETHMOIDAL) BLOCK

The ethmosphenoid shield is the widest at the level of the preorbital corners (Fig. 2A, B). The anterior surface of the snout is almost vertical. The external nostrils (exno) are elliptical in shape and their long axis is horizontal, they are situated slightly anteriorly and dorsally to the apex of the subnasal corner and are visible from above. The premaxillary margin is slightly sinusoidal in outline, its medial part being projected ventrally. The lacrimo-maxillary overlap area (lm oar) is almost twice higher than long. The dermal bones of the ethmosphenoid shield are fused, without any trace of suture, with the exception of the median suture between the parietals, caudally to the pineal foramen (pi), supraorbitals 1, 2 (so1, 2) and intertemporal (it). The pineal foramen is situated in the middle of the orbital division opposite the anterior ends

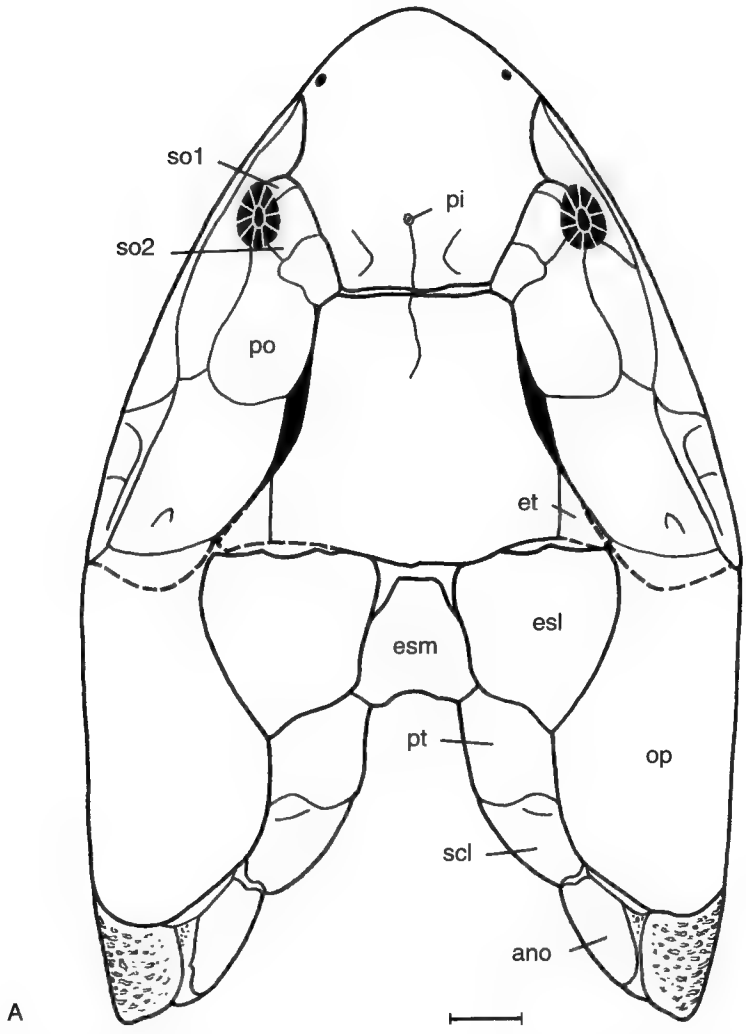

FIG. 1A. — *Medoevia lata* n. g., n. sp., reconstruction of the skull and shoulder girdle in dorsal view. Scale bar: 10 mm.
Medoevia lata *n. g., n. sp., reconstitution du crâne et de la ceinture pectorale en vue dorsale. Échelle: 10 mm.*

of the parietal pit-lines. The pores of the seismo-sensory canal are small, numerous and are distinguishable only in the anterior part of the ethmosphenoid shield.

The toothed part of the naso-rostropremaxilla bears a row of about 15 small teeth (Fig. 2B). The medial tooth pair is slightly bigger than the others, as in *Megistolepis* (VOROBYEVA, 1977a), *Gogonasus* (LONG, 1985b, 1987) and *Chrysolepis* (LEBEDEV, 1983). The palatal lamina

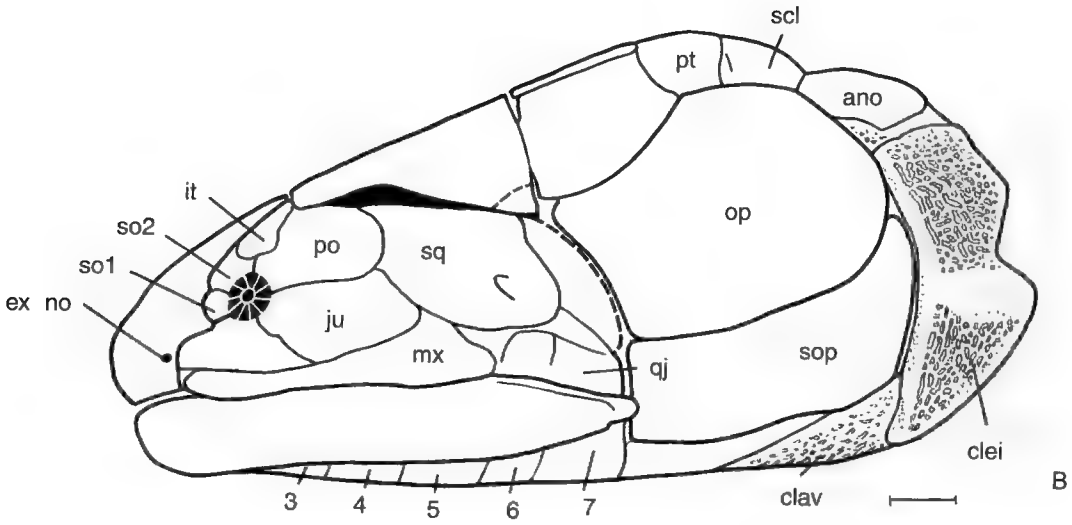

FIG. 1B. — *Medoevia lata* n. g., n. sp., reconstruction of the skull and shoulder girdle in lateral view. Scale bar: 10 mm.
Medoevia lata *n. g., n. sp., reconstitution du crâne et de la ceinture pectorale en vue latérale. Échelle : 10 mm.*

of the naso-rostropremaxilla forms medially two symmetrical, short tongue-like processes, which support a prominent ridge separating the prenasal pits of the ethmoid. Laterally to these processes the palatal lamina is insignificantly developed, except for the medial processes for the sutural contact with the vomers.

The lateral edges of the ethmosphenoid shield are much abraded and no overlapping surfaces with the supraorbitals 1 and 2 can be observed. The posterior tectal is fused to the shield without any trace of a suture. The supraorbital 1 (Fig. 3A, B) is a short rectangular plate bearing a rugosity in the anterior half of its medial surface. A group of small pores of PAUL's organ (Pao) [This term, introduced by VOROBYEVA & LEBEDEV (1986) in honour of Estonian paleontologist V. PAUL, who first described the groups of small sensory pores in *Osteolepis* sp. (*Gyroptychius pauli* Vorobyeva, 1977) (PAUL, 1940)] is situated in the middle of its lateral surface. The supraorbital 2 (Fig. 3C, D) is generally arch-shaped, with a process that wedges between the anterior margin of the intertemporal and the parietal. The supraorbital sensory line canal enters this bone from the parietal at the anterior margin and curves, passing to the intertemporal from the medial side of the dorsal process of supraorbital 2.

The intertemporal is irregularly trapezoidal in shape (Fig. 3E, F). It possesses two pointed processes for overlapping: an anterior one for the supraorbital 2 (so2 ar) and a posterior one for the postorbital (po ar).

The vomer (Figs. 1D, 4A-D; vo) is a rectangular plate with a high, curved tooth-bearing lamina on its ventral side. The anterior border of the vertical lamina (vvl) is situated below the anterior border of the parasphenoid (pa) and the dorsal, flat tongue-like anteromedial processes

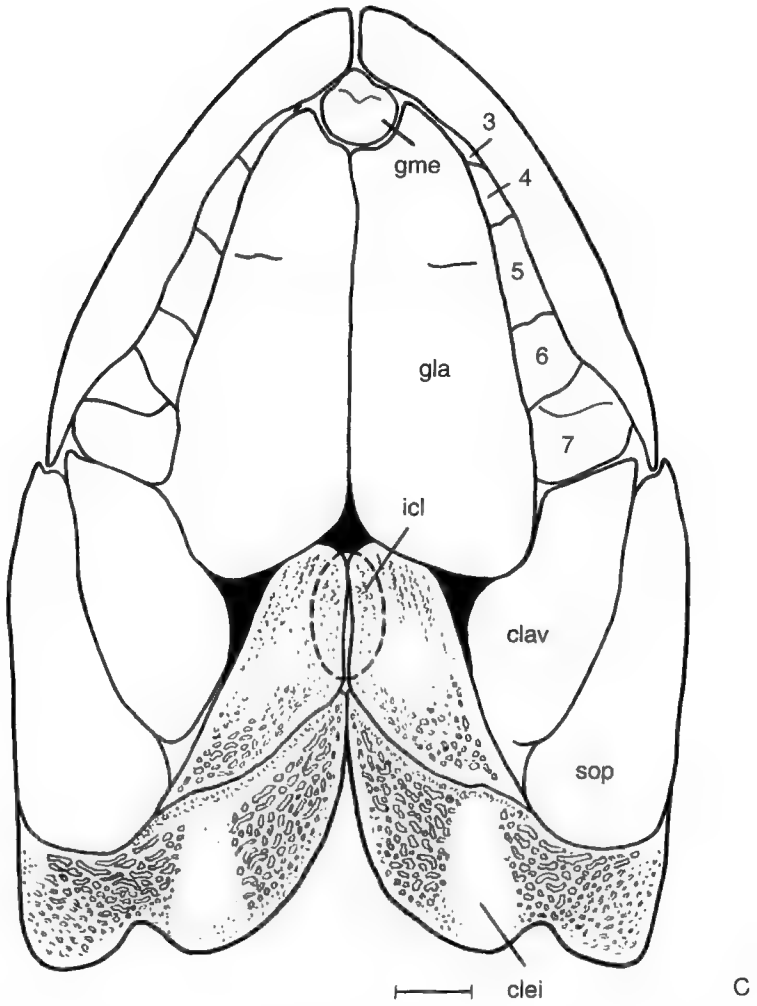

FIG. 1C. — *Medoevia lata* n. g., n. sp., reconstruction of the skull and shoulder girdle in ventral view. Scale bar: 10 mm.
Medoevia lata *n. g., n. sp., reconstitution du crâne et de la ceinture pectorale en vue ventrale. Échelle : 10 mm.*

(vam pr) almost come in contact in the midline and cover the area between it and the posterior edge of the prenasal pits (pn pi), thus forming the posterior margin of the anterior palatal fossa (Fig. 2B). The anterolateral process (val pr) forms a short and massive sutural contact with the lateral process of the palatal lamina of the naso-rostropremaxilla, and thus the anterior margin of the exochoanal passage. The lateral side of the vertical lamina is a continuation of the dorso-medial articulation facet of the ethmoid and its lateral surface is rugose (Fig. 2E, F). The lateral surface of the posterior portion of the vertical lamina forms the medial wall of a conspicuous

FIG. 1D. — *Medoevia lata* n. g. n. sp., mounted braincase and left upper jaw in ventral view. Scale bar: 10 mm.
Medoevia lata *n. g., n. sp., neurocrâne et mâchoire supérieure gauche montés, en vue ventrale. Échelle : 10 mm.*

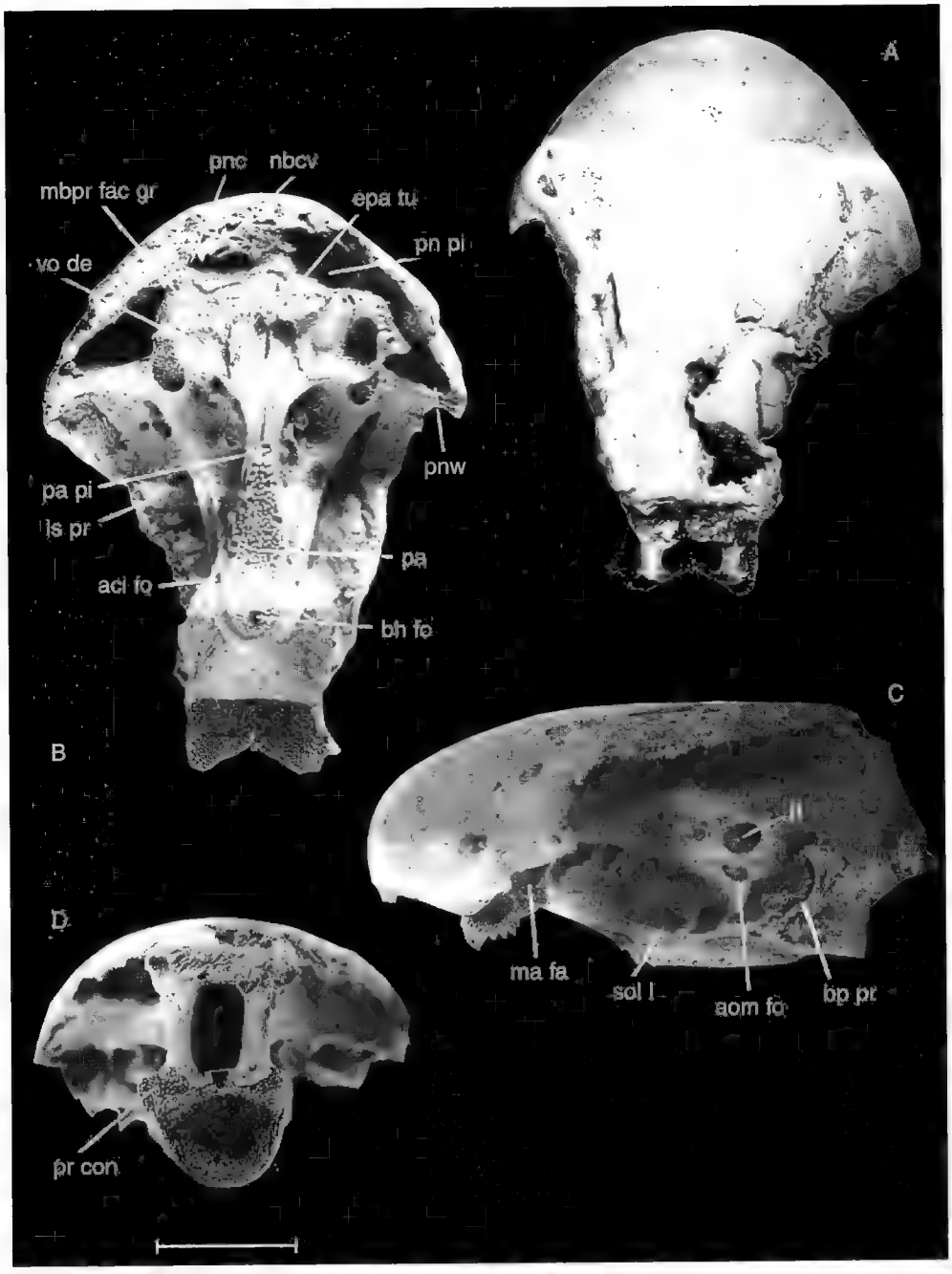

FIG. 2A-D. — *Medoevia lata* n. g., n. sp. Ethmosphenoid block. A, dorsal view; B, ventral view; C, lateral view; D, posterior view. Scale bar: 10 mm.

Medoevia lata *n. g., n. sp., bloc ethmosphénoïdien. A, vue dorsale ; B, vue ventrale ; C, vue latérale ; D, vue postérieure. Échelle : 10 mm.*

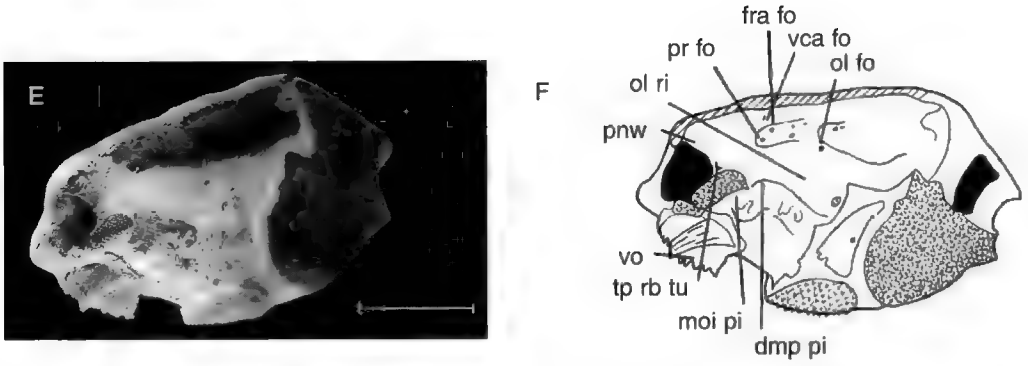

FIG. 2E, F. — *Medoevia lata* n. g., n. sp. Ethmosphenoid block, posterior ventrolateral view. Scale bar: 10 mm.
Medoevia lata *n. g., n. sp., bloc ethmosphénoïdien en vue ventrolatérale postérieure. Échelle : 10 mm.*

fenestra exochoanalis, together with the anterior process of the dermopalatine, with which it forms a vertical sutural junction. The ventral edge of the vertical lamina bears a posterior row of the comparatively large teeth and 2-3 anterior rows of small ones. The ventral portions of the anterior part of the vertical lamina meet together medially, forming a large intervomerine canal (ivc). Its dorsal wall is mainly formed by the ventral surface of the ethmoid.

The exochoanal passage (Fig. 1D) is difficult to see on the photograph because of the displacement of the elements during fossilization. The maxilla and adjoining dermopalatine are shifted to the right side, so that there is no clear contact between their anterior ends and the naso-rostropremaxillary and vomer respectively. Nevertheless, the loose bones on the right side of the head show contact areas and, when put together, clearly shows a large, elongated, and functional exochoanal opening. This contradicts the widespread opinion about the absence a choana in osteolepiforms (for example, ROSEN *et al.*, 1981).

The anterior part of the parasphenoid is bifid, divided by a narrow slit until the level of the posterior margin of the vomers. A sharp crest supports the denticulated plate of the parasphenoid rostrally and the anterior corner of the plate bears a small pit; the bottom of which is rugose. The function of this pit is uncertain (pa pi). The denticulated plate itself is rather short and wide, its length being about 2.5 times more than its maximum width. The small orifice of the bucco-hypophyseal foramen (bh fo) is situated close to the posterior margin of the denticulated plate.

SCLEROTIC RING ELEMENTS

Nineteen loose sclerotic ring elements have been found. Their breadth is so variable that it is possible that the left ring comprised a different number of elements than the right one, as suggested by some plates showing incomplete fusion (Fig. 3G, H). The elements are rectangular

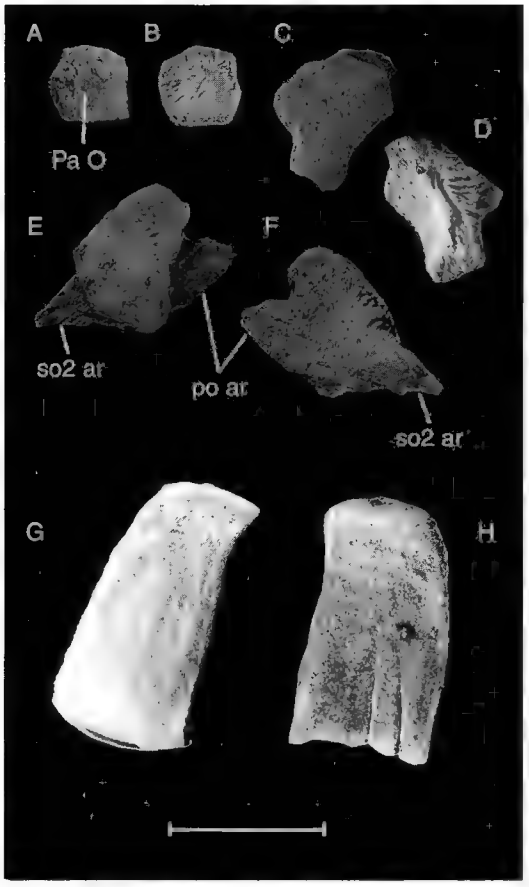

FIG. 3. — *Medoevia lata* n. g., n. sp. Dermal bones of the ethmosphenoid shield and the sclerotic ring elements. A, B, supraorbital 1; C, D, supraorbital 2; E, F, intertemporal; G, H, sclerotic elements. A, C, E, G, lateral views; B, D, F, H, medial views. Scale bar: 10 mm, except for G and H: 1.5 mm.

Medoevia lata *n. g., n. sp. Os dermiques du bouclier ethmosphénoïdien et éléments de l'anneau sclérotique. A, B, supraorbitaire 1; C, D, supraorbitaire 2; E, F, intertemporal; G, H, éléments de l'anneau sclérotique. A, C, E, G, vues latérales; B, D, F, H, vues médiales. Échelles: 10 mm, sauf pour G et H: 1,5 mm.*

in shape, curved and almost smooth on both surfaces, except for poorly marked grooves parallel to the margins. Their inner and the outer edges are slightly rounded.

NEUROCRANIAL COMPONENT OF THE ETHMOSPHENOID DIVISION

The neurocranium is well ossified. The length of the ethmoid represents about 1/3 of the total length of the ethmosphenoid. The interorbital wall is deepest above the parasphenoid (Figs. 2C, 5).

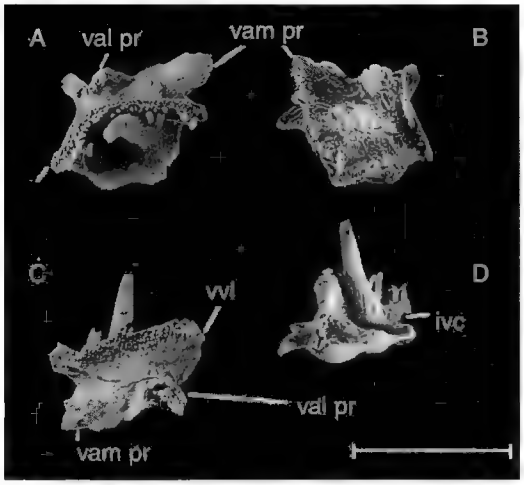

FIG. 4. — *Medoevia lata* n. g., n. sp. Right vomer. A, ventral view; B, dorsal view; C, anterior view; D, posterior view. Scale bar: 10 mm.

Medoevia lata *n. g., n. sp. Vomer droit. A, vue ventrale; B, vue dorsale; C, vue antérieure; D, vue postérieure. Échelle: 10 mm.*

The prenasal pits (Fig. 2C) are much deeper than in *Eusthenopteron* (JARVIK, 1942, 1980). The lateral wall of the pit is occupied by the orifice of the ventral branch of the nasobasal canal (nbcv), which also shows the more anterior course of its lateral (?) branch. The anterior orifice of the palato-nasal canal (pnc) is situated slightly behind the foramen of the ventral branch of the nasobasal canal and may be traced between the ventral surface of the ethmoid and the dorsal surface of the vomerine process of the palatal lamina of the naso-rostropremaxillary.

The ventral surface of the ethmoid region in *Medoevia* is much shorter and broader than in *Eusthenopteron* (JARVIK, 1942), so that the pits for the dorsal, thickened part of the vomers (vo de) are not situated anteriorly to the anteromedial articulation surface for the palatoquadrate, but opposite to it. The anterior process of the parasphenoid becomes very closely fused to the ventral surface of the ethmoid, and there is a small, well marked median tubercle between its two branches. This boss (epa tu) is situated dorsally to the junction of the medial parts of the vertical laminae of the vomers, and its function is unclear. The depression for the vomers bears a groove (mbpr fac gr), running rostro-caudally along the lateral margin of the anterior processes of the parasphenoid. This groove may represent the canal for the medial branch of the palatal ramus of the n. facialis.

The posterior surface of the ethmoid is subdivided into the dorsolateral and medioventral parts by the massive olfactory ridge (ol ri; Fig. 2E, F). It continues backwards up to the foramen for the n. opticus (II), and lies ventrally to it; anteriorly it bears the medial articular facet (ma fa) for the process of the palatoquadrate, and immediately laterally to it, at the ventral edge of

the postnasal wall (pnw), there is a small rugose tubercle, that might have served for the attachment of the transverse portion of the m. retractor bulbi (tp rb tu).

The dorsolateral part is, in its turn, subdivided into dorsomedial and dorsolateral areas by the buttress of the lateral supraorbital lamina, or the dorsolateral ridge (dl ri). The dorsolateral ridge passes backwardly to the lateral surface of the interorbital wall and joins the olfactory ridge in front of the foramen for the optic nerve. The lateral supraorbital process (ls pr) is flattened and only slightly convex, in contrast to *Eusthenopteron*, where it is almost rounded in transverse section (JARVIK, 1942). It runs postero-laterally along the ventral surface of the dermal roofing bones, but the continuation of this process is destroyed. The dorsomedial area is a deep, anteriorly directed depression. Its anterior wall is pierced by several foramina, the most conspicuous of which is situated at the dorsolateral corner, or just ventrally to the dorsolateral ridge, depending from the side of the specimen, and may represent the posterior orifice of the canal for the r. ophtalmicus lateralis (ol fo).

The dorsolateral area is a large, anteriorly directed pit, which contains another smaller elliptical pit in the dorsomedial part of its anterior wall; the latter is pierced by two large and 3-4 smaller foramina. The ventralmost large foramen is the back of the funnel-shaped canal for the main branch of the n. profundus (pr fo), that opens in the nasal cavity dorsolaterally to the foramen for the olfactory canal. There are two foramina on the right-hand side, which might be interpreted as the openings of the canal for the r. frontalis anterior of the n. profundus: the first one is situated dorsolaterally to the main foramen and the second one slightly ventrolaterally. The left-hand side shows only one dorsolateral foramen, which is more probably for the nerve mentioned above (fra fo). The other foramina situated in the elliptical pit, may be for the other (possibly dorsal) branches of the profundus nerve, as in *Thursius estonicus* (VOROBYEVA, 1977a). A small foramen, dorsolaterally to this group, may represent the passage for the v. cerebralis anterior (vca fo), as in *Thursius estonicus* (VOROBYEVA, 1977a).

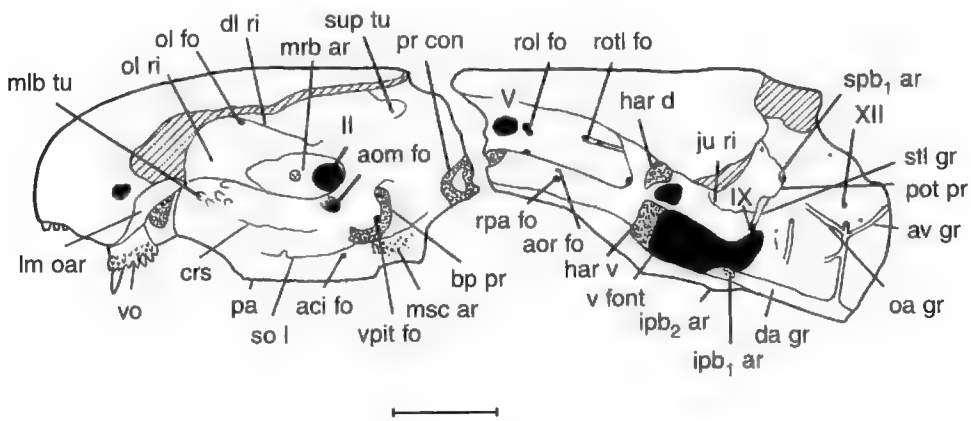

FIG. 5. — *Medoevia lata* n. g., n. sp. Drawing of the ethmosphenoid and otico-occipital blocks in lateral view. Scale bar: 10 mm.

Medoevia lata *n. g., n. sp. Dessin des blocs ethmosphénoïdien et otico-occipital en vue latérale. Échelle: 10 mm.*

The postnasal wall is short and the orbitonasal canal passed by the shallow notch (onc n) of its medial part; the lateral edge of the passage is lined by the shallow notch at the tip of the medio-dorsal process of the maxilla, its medial edge by the dorsal side of the anterior end of the dermopalatine and the lateral side of the anteromedial articulation buttress of the autopalatine. The ventral edge of the postnasal wall is situated at the level of the midpart of the facet for the medial ethmoid articulation of the palatoquadrate.

The position of the orbitonasal canal varies among osteolepiforms. It may be a large opening, where the postnasal wall is deep, as in *Eusthenopteron foordi* (JARVIK, 1937, 1942, 1966, 1980), *Thursius estonicus* (VOROBYEVA, 1977a), or, if it is short, as a notch in the medial part of the postnasal wall, as in *Jarvikina wenjukowi* (PIN 54/121, PIN 2986/2), *Eusthenopteron obruchevi* (PIN 1737/42), *Shirolepis ananjevi* (PIN 782/1) (pers. obs.) and probably *Gogonasus* (LONG, 1985b). Accepting the interpretation of this structure as transmitting the orbitonasal vein (MILLOT & ANTHONY, 1958), it may be concluded that its position was variable and has no special phylogenetic meaning.

The medial ethmoidal articulation facet for the palatoquadrate (ma fa) is oval, elongated, with an oblique main axis directed rostro-caudally and dorsoventrally, forming an angle of about 45° to the vertical plane.

In the area bordered by the parasphenoid ventrally, the olfactory ridge dorsally and the basipterygoid process posteriorly, there is a large, shallow, depression, which is subdivided into several pits and bears ridges and tubercles (Figs. 2C, 5). Its anteriormost part is a deep, rounded pit, situated posteromedially to the medial ethmoidal articulation facet.

When the palatoquadrate complex is connected, it is situated above its dorsal surface and might serve the attachment of the m. obliquus inferior of the eyeball (moi pi). There are small tubercles on the anterior edge of the pit on the left-hand side and on its posterior edge on the right-hand side. They may indicate the position of the attachment for aponeuroses. The pit receiving the dorsomedial process of the palatoquadrate (dmp pi) is a rather shallow, elongated structure, which is situated posteroventrally to the pit described above. Its dorsal wall has an area of finely perforated bone and the shallow ridge above it bears 2-4 massive rugose tubercles, that probably housed the attachment of the principal portion of the m. levator bulbi (mlb tu). In contrast to *Eusthenopteron*, the crista suspendens (crs) begins posteriorly to these tubercles and is rather poorly developed. Its posterior end is situated above the basisphenoid articulation.

The interorbital region of the ethmosphenoid is a rather high and thin structure, but thickens posteriorly; its maximum thickness is reached between the basipterygoid and the suprapterygoid processes. This area is half as long as the breadth of the ethmosphenoid shield; that is, approximately the same index as in *Gogonasus* (LONG, 1985b). The suborbital ledge (so l), originating from the junction of the interorbital wall with the parasphenoid, is a sharp-edged ridge, which begins anteriorly to the foramen for the n. opticus and extends backwardly, gradually turning into the basipterygoid process (bp pr). There are two symmetrical projections at the beginning of the ledge, one of which is hook-shaped, and the other is a knob. The foramen for the a. carotis interna (aci fo) lies ventral to the most projecting part of this edge; the latter forms a sharp-edged crest, supporting the basipterygoid process anteriorly. There is a notch between the crest and the processes mentioned above.

The basipterygoid process displays two major facets for the basal process of the palatoquadrate; the dorsal one faces anterolaterally and the ventral one antero-dorsolaterally. The dorsal facet is concave and the ventral one is mostly convex. The lateral surface of the basipterygoid process bears a rugose area for the muscle attachment (m. subcephalicus, msc ar). The most proximal part of this area bears either a small pocket on one side, or a ridge on the other, for the aponeurosis of the superficial ligament of the muscle. The muscle seems to have been paired, as the ventral surface shows no traces of its attachment.

The foramen for the n. opticus (II) is large, situated opposite the dorsalmost end of the basipterygoid process, and slightly in front of its anterior end. The posterior part of the olfactory ridge is occupied by the area of attachment for the m. retractor bulbi (mrb ar), and the foramen for the n. opticus is situated in the middle of its posterior part. The margins of the area are marked by a gentle ridge anterodorsally and a row of tubercles of various sizes posteriorly and ventrally. The midpoint of the anterior portion of the area is occupied by a small patch of bone devoid of the periosteal ossification. Its function is unclear.

The n. oculomotorius (III) might have left the brain cavity through the same foramen as the n. opticus, as in *Osteolepis* (WATSON, 1954), *Gyroptychius pauli*, and *Megistolepis klementzi* (VOROBYEVA, 1977a). The foramen for the n. trochlearis (IV) may be one of the small foramina situated below the exoskeletal roof and above the boss of the suprapterygoid articulation (sup tu).

The foramen for the a. ophtalmica magna is situated in a groove, ventrally to the crista suspendens and in front of the basipterygoid process on the right-hand side. This unusual position, below the dorsal margin of the palatoquadrate is compensated by the subsequent course of the vessel, which passes dorsally via a small groove, crosses the crista suspendens and reaches the margin of the area for the attachment of the m. retractor bulbi; on the left-hand side the corresponding canal is enclosed in a vertical ridge, and opens by a large orifice ventrally to the foramen for the n. opticus (aom fo). The pituitary vein leaves the braincase through a large pituitary foramen situated at the base of the basipterygoid process, anteriorly to it and in a deep pit lying at the level of its midheight (vpit fo).

The processus connectens (pr con; Fig. 2D) is situated rather far caudally from the dorsal part of the basipterygoid process, making the posterior surface of the ethmosphenoid anteriorly inclined at an angle of about 70° to the horizontal plane. Its posterior and lateral surfaces are devoid of periosteal lining, except on a patch in the middle of its lateral surface at the left-hand side. The unossified surface is continued to the bottom of the cranial cavity. The suprapterygoid process (sup tu) is a massive boss, supporting the posterolateral corner of the ethmosphenoid shield. There is a massive, rugose vertical ridge in front of it, which could serve the attachment of the m. levator arci palatini, lining the ascending process of the palatoquadrate anteriorly.

OTICO-OCCIPITAL DIVISION

The otico-occipital block differs in general shape and proportions from that of *Eusthenopteron*, *Megalichthys*, *Ectosteorhachis*, *Osteolepis* and *Megapomus* (JARVIK, 1954, 1972, 1975; ROMER, 1937, 1941; THOMSON, 1965, 1966, 1967; VOROBYEVA, 1977a) (Fig. 6A, B) and is similar in outline to that of *Siphonodus* (Fischer, 1852). The anterior part of this portion is low, the deepest part being at the level of the posterior edge of the skull roof. The major difference with other taxa rests on its outline in ventral view; its maximum width is shortly before the

anterior limit of the occipital region, which, in contrast to the otico-occipital of the five first genera mentioned above, is not diamond-shaped, but trapeze-shaped, with a very broad base.

The dermal bones of the otico-occipital ("parietal") shield are fused, with the exception of the median suture between the two postparietals anteriorly. A short segment of this suture is seen close to the posterior margin of these bones and the well-marked suture between the tabular and extratemporal (et). This suture is supported by the crista parotica, which is broad, so that a large part of the extratemporal is connected with this endocranial structure.

The anterior margin of the shield is almost straight, with only a shallow embayment for the junction with the posterior margin of the parietals; the openings of the infraorbital canals open at this level. There is no overlapped surface for the postorbital, which suggests, that the joint between the postparietal and parietals was kinetic. The spiracular notch looks rather deep, due to the lateral extension of the posterior corners of the shield. The posterior margin of the shield is arched, its medial part being the most convex; it bears a series of shallow pocket-like notches for the contact with the extrascapulars.

The median extrascapular (esm) is much smaller than the lateral ones (esl) (Fig. 6C-F). The lateral extrascapular-otico-occipital length ratio is 0.70, that is, the highest among osteolepiforms, except *Marsdenichthys*, in which this index is 0.8.

NEUROCRANIAL COMPONENT OF THE OTICO-OCCIPITAL DIVISION

Neither the lateral occipital, nor the ventral otic fissures are preserved in the adult stage in *Medoevia* (the gaps on both sides of the specimen (Figs. 1D, 6B) are cracks, with some bone missing on the right-hand side and being out of contact on the left side), although the vestibular fontanelle (v font) is rather large. Its shape and extension is similar to that observed in *Megapomus heckeri* Vorobyeva, 1977a, and contrasts to that in *Megalichthys* Romer, 1937, where it is completely ossified. The length of the basicranial fenestra (bc fen) is about one half of the total length of the otico-occipital division. The temporal region is rather long and narrow and the otic capsules are shifted backwards and laterally in comparison to those in *Eusthenopteron*.

The post-temporal fossae (ptf) are comparatively short due to the shift of the otic region backwards. The endochondral roofing of the fossae is almost complete, with the exception of a narrow strip of the free exoskeleton of the ventral side of the skull roof. The walls of the post-temporal fossae are rather rugose, suggesting that it served the insertion of the epaxial trunk muscles (Fig. 6G, H). The curved groove in the floor of the fossae may be interpreted as the passage for the r. supratemporalis lateralis (stl gr), which pierces the floor of the post-temporal fossa in *Amia* (JARVIK, 1980). In *Medoevia*, this groove passes from the posterior edge of the fossa forwards along its medial side, crosses it suddenly in its middle and then runs in the laterally towards a large posterior foramen of the spiracular canal (spcpo fo). There is a smaller orifice postero-laterally to it, which is connected with the former by a short groove or a canal, overlain by a short bar. There are two large foramina in the anterior wall of the post-temporal fossa in *Megapomus*, described by VOROBYEVA (1977a), and interpreted as a paired canal for the r. oticus VII and a posterior diverticle of the spiracular organ; in *Medoevia*, it is proposed that the large canal housed the posterior diverticle of the spiracular canal and the r. oticus VII (spcpod + ro fo), and the smaller foramen transmitted the r. supratemporalis lateralis, which passes to the crista parotica in *Eusthenopteron* (JARVIK, 1980).

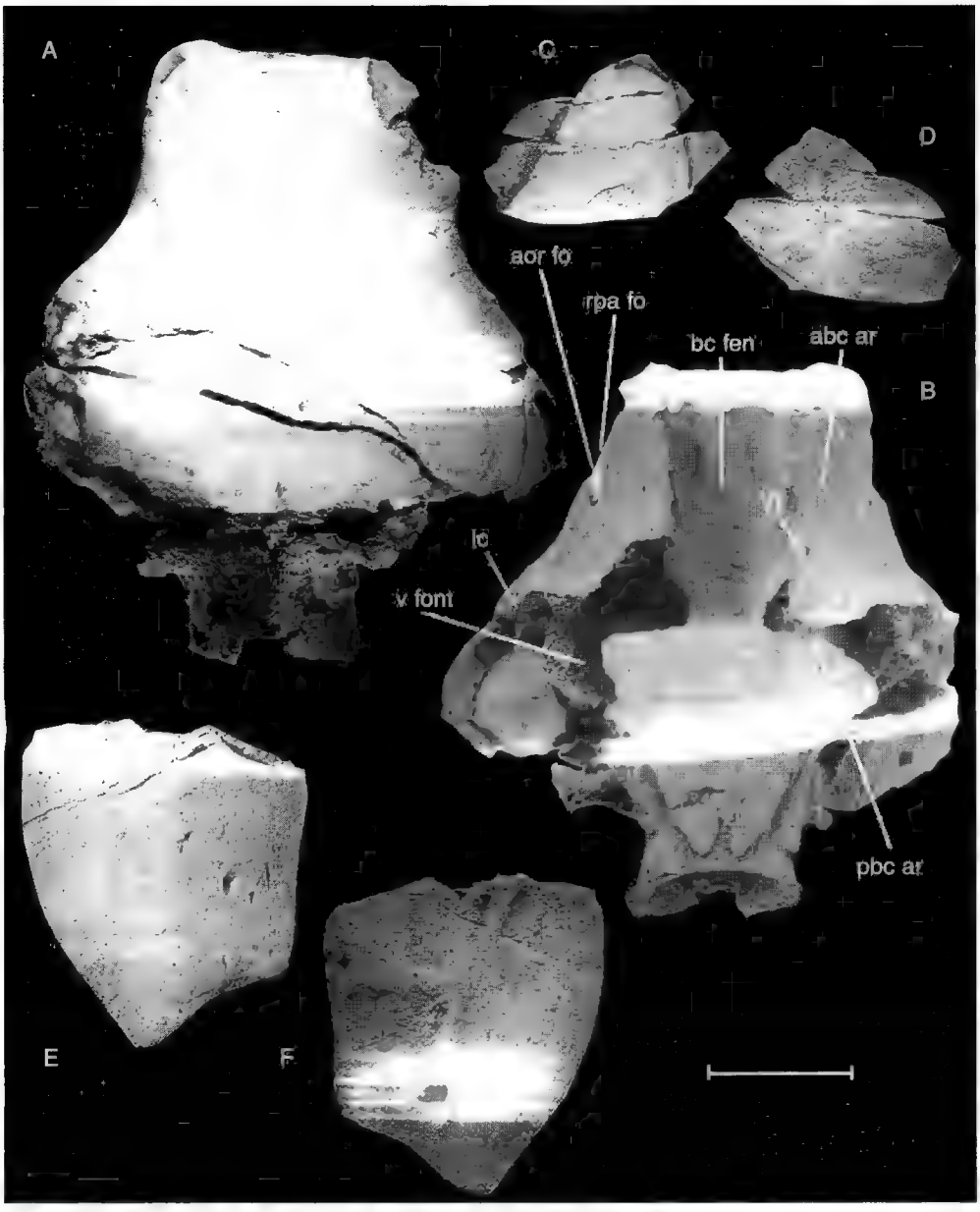

FIG. 6A-F. — *Medoevia lata* n. g., n. sp., otico-occipital division. A, B, G, H, otico-occipital block; C, D, median extrascapular; E, F, lateral extrascapular. A, C, E, dorsal view; B, D, F, ventral view. Scale bar: 10 mm.

Medoevia lata *n. g., n. sp., division otico-occipitale. A, B, G, H, bloc otico-occipital ; C, D, extrascapulaire median ; E, F, extrascapulaire latéral. A, C, E, vue dorsale ; B, D, F, vue ventrale. Échelle : 10 mm.*

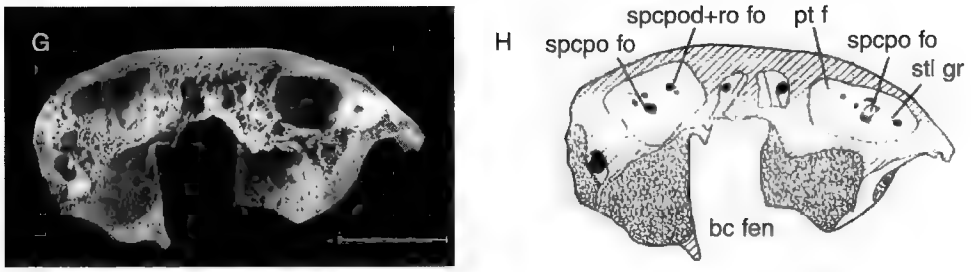

FIG. 6G, H. — *Medoevia lata* n. g., n. sp., oblique cross-section through the subtemporal fossae of the otico-occipital block in posterior view. Scale bar: 10 mm.

Medoevia lata *n. g., n. sp., section transversale oblique à travers les fosses subtemporales du bloc otico-occipital en vue postérieure. Échelle : 10 mm.*

The median paratemporal articular area, i.e. the anteroventral corner of the otico-occipital block is, as in *Eusthenopteron*, devoid of periosteal lining, and accommodated the processus connectens of the ethmosphenoid. The contact of the posterior tips between the connecting processes with the temporal walls is marked by the vertical extension of the spongy articulation area and by the corresponding ventral protrusion of the antero-medial corner of the ventral surface. The articulation area is continued backwards by the ventral edge of the medial walls of the basicranial fenestra and no doubt served the cartilaginous junction with the arcuals. The lateral surface of the otic shelf (Fig. 5), which is equally deep along its entire length and straight, in contrast to that of *Eusthenopteron* and *Megalichthys*, where it curves ventrally, and bears a group of several small and one large foramina. Ventrally to this area, on the ventral surface, there is one more large opening. These may be interpreted as the foramina for the r. palatinus VII (rpa fo) and the orbital artery (aor fo).

The facialis canal runs postero-ventrolaterally, gives off the canal for the r. palatinus, and then opens in the floor of the jugular canal medially to the lateral commissure. The otic shelf is most prominent anteriorly; there, the bottom of the jugular groove is pierced by the large orifice for the v. cerebralis media. The largest orifice in the lateral wall of the cranial cavity is the trigeminus (V) foramen, which is separated from the intracranial slit by a thick bar forming the anterior edge of the wall. Close to it, and posteriorly, there is a smaller orifice, which is single on the right-hand side and double (8-shaped) on the left-hand one, and could transmit the r. ophtalmicus lateralis (rol fo). These two foramina are situated in a shallow depression between the deep, postero-medially directed pocket for the m. levator arci palatini and the jugular groove (ju gr). The ventral and lateral walls of the pocket are strongly rugose and its posterodorsal corner is pierced by a small foramen, probably for the orbital artery, which descended from the groove for the occipital artery. The posterior wall of the pocket for the m. levator arci palatini is pierced dorsally, right at the limit between the ventral surface of the dermal shield and the dorsal surface of the endocranium, by a small foramen. This foramen is probably for a branch

of the r. oticus lateralis, which lies close to the pit for the spiracular sense organ. This pit is situated dorsomedially in the anterior wall of the otic capsule. The orifice of the anterior canal of the r. oticus lateralis (rotl fo) is situated above the jugular groove and anteriorly to the ventral orifice for the spiracular canal. It is connected with the latter by a distinct, backwardly running groove.

The jugular canal is continued backwards, and limited dorsally by a sharp-edged jugular ridge (ju ri) which continues backwards almost to the articulation knob for the suprapharyngobranchial 1 (spb1 ar). They are separated by a vertical groove for the r. supratemporalis lateralis (stl gr), arising dorsally from the glossopharyngeus (IX) foramen. The articulation facet just mentioned occupies the postero-ventrolateral surface of the postotic (pot pr) process. In contrast, the articular areas for the infrapharyngobranchials 1 (ipb1 ar) and 2 (ipb2 ar) are covered with perichondral bone and are represented by small tubercles situated as in *Eusthenopteron*, behind the vestibular fontanelle and at the level of the ventrolaterally directed process lying ventrally to the edge of the basicranial fontanelle.

The groove for the dorsal aorta (da gr) passes anteriorly to the lateral surface of the otic capsule and obviously ran against the surface of the cartilage of the otic capsule. The dorsal and ventral articular areas for the hyomandibula are situated as in other osteolepiforms, that is, ventrally and dorsally to the jugular canal, on the posterior surface of the lateral commissure (lc). A tubercle with a rough surface, probably for the m. adductor hyomandibulae, is situated anteriorly to the ventral articular area (BJERRING, 1971).

In contrast to the condition in *Megapoma*, the groove for the dorsal aorta does not give off an enclosed canal for the occipito-vertebral artery, but a vertical groove running dorsally along the lateral surface of the occipital. This groove gives off anteriorly and posteriorly branches which enter a small foramen dorsolaterally. A short canal for the occipital artery (oa gr) runs anterodorsally from this point to meet a small pit between the lateral occipital surface and the foramen for the n. vagus (X), which opens on the posterior surface medial to the postotic process. Dorsally, the groove for the occipital artery runs along the lateral surface and leads to a small foramen situated ventrolaterally to the occipital plug. Two smaller foramina lie in front of the origin of the groove for the occipital artery, the posterior one being joined by a groove of the same system of branching grooves for blood vessels. JARVIK (1980) describes in the same position two small foramina in *Eusthenopteron*, and calls them the canals for the "spino-occipital nerves". The rearmost of these two foramina is found in a similar position in *Megalichthys* (ROMER, 1937) and is suggested to transmit the n. hypoglossus (XII). The groove for the vertebral artery (av gr) is seen only on the right side; it leaves the occipito-vertebral groove and passes posterodorsally to the edge of the braincase.

Approximately at the midlength of the basicranial fenestra. The canal for this nerve originates in the antero-ventromedial part of the floor of the otic capsule and passed through it.

There are two surfaces for the attachment of the basis cranii muscles (Fig. 6B). The anterior one (abc ar) has the shape of a triangle whose angles are situated respectively at the anterior tip of the basal plate of the otoccipital anteriorly, the abducens nerve foramen laterally, and the edge of the ventral hyomandibular facet medially. Its lateral side is represented by the edge of the otic shelf. The second muscle attachment area (pbc ar) is situated posteromedially to the first one and occupies the space limited by the vestibular fontanelle laterally, the basicranial

fontanelle anterolaterally, and a well-marked ridge, which continues the lateral edge of the latter posteriorly up to the level of the tubercle for the attachment of the infrapharyngobranchial 2, and then runs laterally towards the groove for the dorsal aorta. The anterior depression probably housed the insertion of the subcephalic muscle and the posterior one, as pointed out by VOROBYEVA (1977a), could accommodate the insertion of its antagonist. JARVIK (1980) suggested the presence of a series of basicranial muscles, from 1 to 6, and noted that corresponding muscles (basicranial 4 and 5) are found in the embryonic stages of modern amphibians and, probably, in the adults of some extinct fishes (JARVIK, 1972). Another possible interpretation is that it housed the insertion of the palatoquadrate depressor or levator of the branchial arches.

The ventral wall of the brain cavity, which is ossified in the posterior half of the otico-occipital block bears anteriorly a narrow strip devoid of periosteal lining dorsally and bordered by its sharp rising edges laterally. Caudally, this ridge becomes wider and the periosteal layer turns into a funnel which leads to paired canals, running posteroventrally from the brain cavity. The posterior surface of the ventral wall of the brain cavity is totally devoid of periosteal lining. JARVIK (1980) reconstructs a median basilar artery, but it is possible, that this artery was paired and occupied a groove laterally. The canal runs toward a foramen in the lateral surface of the occipital division, which is situated before the emergence of the occipital artery from the occipito-vertebral artery, and this canal may thus have housed the commissure between the occipito-vertebral and basilar arteries. The median structure might serve for the attachment of the brain membranes.

In contrast to *Eusthenopteron*, only one (suprachordal) arcual plate was ossified in *Medoevia*. It is a wide and short, rectangular ossification (Fig. 7A-C) whose dorsal surface is smooth, except in a medial, unossified area similar to that of the floor in the posterior part of the brain cavity, yet a little broader. The lateral surfaces are almost rectangular and blunt, and contacted with the spongy surfaces on the medial sides of the ventral part of the temporal wall. The ventral surface of the arcual plate is concave to cover the notochord.

The dorsal wall of the braincase in *Medoevia* is uneven, possibly due to the attachment for the brain membranes. There is a pair of small pits in its antero-lateral corners, which give rise to the shallow grooves running posteriorly up to the point situated slightly behind the foramen for the r. ophtalmicus lateralis. This area corresponds to the mesencephalon and the paired impressions might be due to the lobi optici. Starting from this point the rugosity of the surface increases and, behind the sinus superior, the width of the dorsal surface decreases twice. There appears a double groove, both branches of which unite to pass caudally. This groove reaches a large funnel-shaped foramen of a vertical, unpaired canal which is displaced to the right and extends to the supraotic cavity. Behind it, the dorsal wall of the cavity slopes down, as its lateral

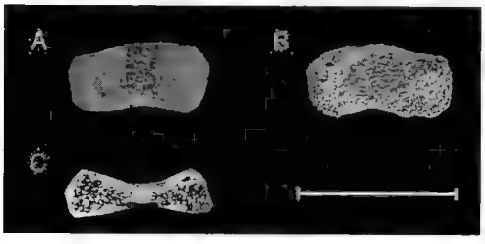

FIG. 7. — *Medoevia lata* n. g., n. sp., arcual plate. A, dorsal view; B, ventral view; C, anterior view. Scale bar: 10 mm.

Medoevia lata *n. g., n. sp., plaque arcuale. A, vue dorsale ; B, vue ventrale ; C, vue antérieure. Échelle : 10 mm.*

walls come closer to each other, thereby marking the posterior surface of the cerebellum. Ventrally to it the lateral wall is pierced by the foramen for the n. vagus (X) and the n. liniae lateralis, which pass through a common canal. Ventrally, a smaller foramen penetrates the ventrolateral wall of the brain cavity and may be for the hypoglossus canal. The short and thin glossopharyngeus canal penetrates the posterolateral part of the wall of the otic cavity.

The medial wall of the otic cavity is, as in *Eusthenopteron*, unossified. The general pattern of the semicircular canals, ampullae, utriculus diverticle and sacculus is the same as in the latter, except for its position in relation to the supraotic canals. The sinus superior is situated opposite the ventral orifice of the anterior dorsal canal issued from the supraotic cavity, while in *Eusthenopteron* it is situated behind the sinus. The anterior canals of the supraotic cavity are narrower than in *Eusthenopteron* and the median wall between them disappears only at a short distance after the anterior extremity of the posterior vertical semicircular canal.

Dermal bones of the cheek plate

The anterior edge of the medial surface of the postorbital (Figs. 1A, B, 8A, B; po) shows a large opening for the sensory line canal (iosc fo), which is bordered posteriorly by a sharp-edged crest runing ventrally towards the overlapping surface for the supraorbital 2. Dorsally, this crest forms a small platform, which serves for the contact with the posterior process of the intertemporal (it ar). The anteroventral corner bears short crests which are parallel to the orbital margin. These crests are prolonged onto the orbital margin and posteroventrally onto the jugal (ju). This bone (Figs. 1A, B, 8C, D) is rather long and participates to the orbital margin. Sensory canals enclosed within the bone are marked by ridges on its medial surface. The ossification center bears several large and numerous small nutrient pores. The squamosal (Figs. 1A, B, 8E, F; sq) is diamond-shaped, and displays the general osteolepid condition. Its pit line is situated rather far dorsally from the ventral margin, bifurcates dorsally on the right-hand side. The quadratojugal pit-line (Figs. 1A, B, 8G, H; qj) is arch-shaped, starting anteroventrally and then extends posterodorsally. In its middle part, it gives off a ventral branch which almost reaches the bone margin. The dorsal maxillary process (Fig. 8I, J; dmax pr) is directed anterodorsally. The notch between the latter and the anterior process of the maxilla forms the posterior wall of the exochoana. The medial surface of the dorsal maxillary process and the maxilla itself bear a junction surface for the lateral side of the dermopalatine. The alar process is rather well developed and extends backwardly up to level of the deepest portion of the bone.

Palatoquadrate and associated plates

The palatoquadrate in *Medoevia* agrees in many respects with that of *Osteolepis macrolepidotus* (Watson, 1954), the general configuration and major articulation areas being very similar (Fig. 9A-E), and, conversely, they differ from those in the Middle Devonian *Thursius estonicus* and *Gyroptychius pauli*, described by Vorobyeva (1977a). The palatoquadrate complex of *Eusthenopteron foordi* (Holmgren & Stensio, 1936; Jarvik, 1942, 1944a, 1954, 1980) is somewhat longer, the ascending process being displaced far backwards.

The vertical dermopalatine plate is almost twice as long as its horizontal plate (Fig. 10A-D). The anterior process of its vertical lamina is jointed to the posterior edge of the vertical plate

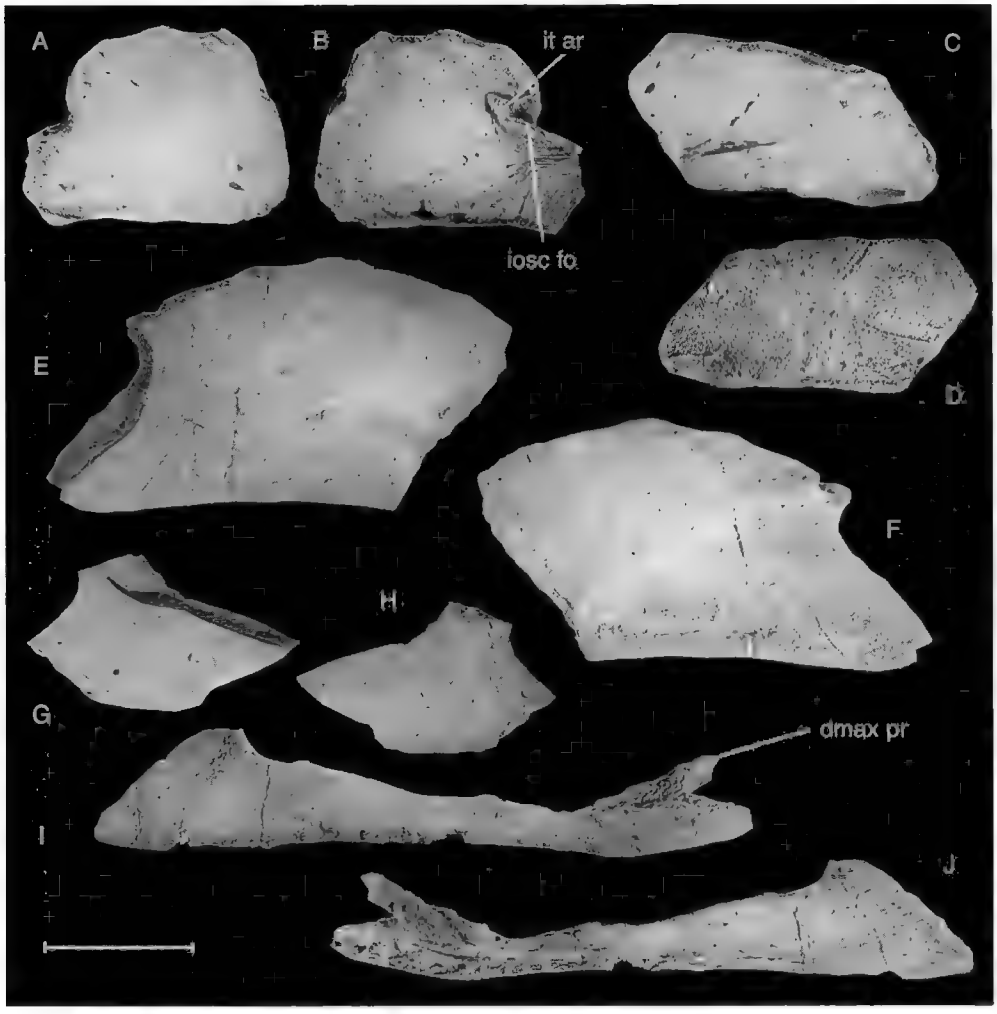

FIG. 8. — *Medoevia lata* n. g., n. sp., dermal bones of the cheek plate. A, B, postorbital; C, D, jugal. E, F, squamosal; G, H, quadratojugal; I, J, maxilla. A, C, E, G, I, lateral view; B, D, F, H, J, medial view. Scale bar: 10 mm.

Medoevia lata *n. g., n. sp., os dermiques de la joue. A, B, postorbitaire ; C, D, jugal. E, F, squamosal ; G, H, quadratojugal ; I, J, maxillaire. A, C, E, G, I, vue latérale ; B, D, F, H, J, vue médiale. Échelle : 10 mm.*

of the vomer by a suture. The vertical lamina is deepest opposite the fang pair, where its ventral edge bears a row of rather large denticles. The dentition of its other parts consists of the 2-3 rows of smaller teeth. The anterior process lines dorsally a large pit in the endoskeletal bone, which houses the tip of the coronoid fang, and makes a notch in the anterior margin of the horizontal plate. The similar, yet shallower, pit for another coronoid fang is lined by the posterior

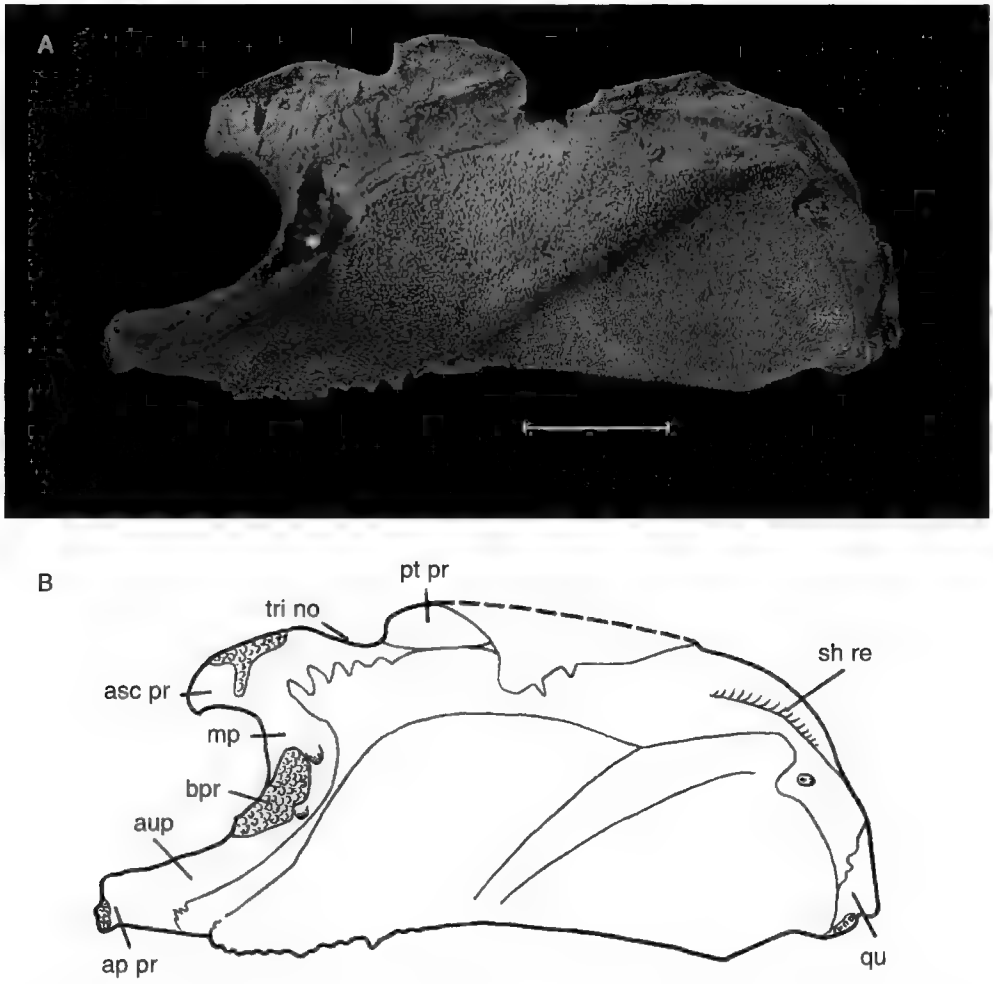

FIG. 9A, B. — *Medoevia lata* n. g., n. sp., palatoquadrate complex. A, B, medial view. Scale bar: 10 mm.
Medoevia lata *n. g., n. sp., complexe palatocarré. A, B, vue médiale. Échelle : 10 mm.*

margin of the dermopalatine and the anterior margin of the ectopterygoid. There is only one pair of fangs on the ectopterygoid, and the posterior portion of the ventral surface of the horizontal lamina is flat. The dermal lining of the pit for the third pair of coronoid fangs is pierced by a rounded orifice in the middle of the horizontal lamina of the ectopterygoid.

The posterior palatonasal canal (ppal fo) pierces the dorso-lateral ridge of the dermopalatine and comes out to its dorsal surface to be continued forwards by the anterior palatonasal canal. The groove for the postchoanal anastomosis (pca gr) follows the dorsal part of the anterior process of the dermopalatine towards the small notch on its medial margin, then it turns backwards.

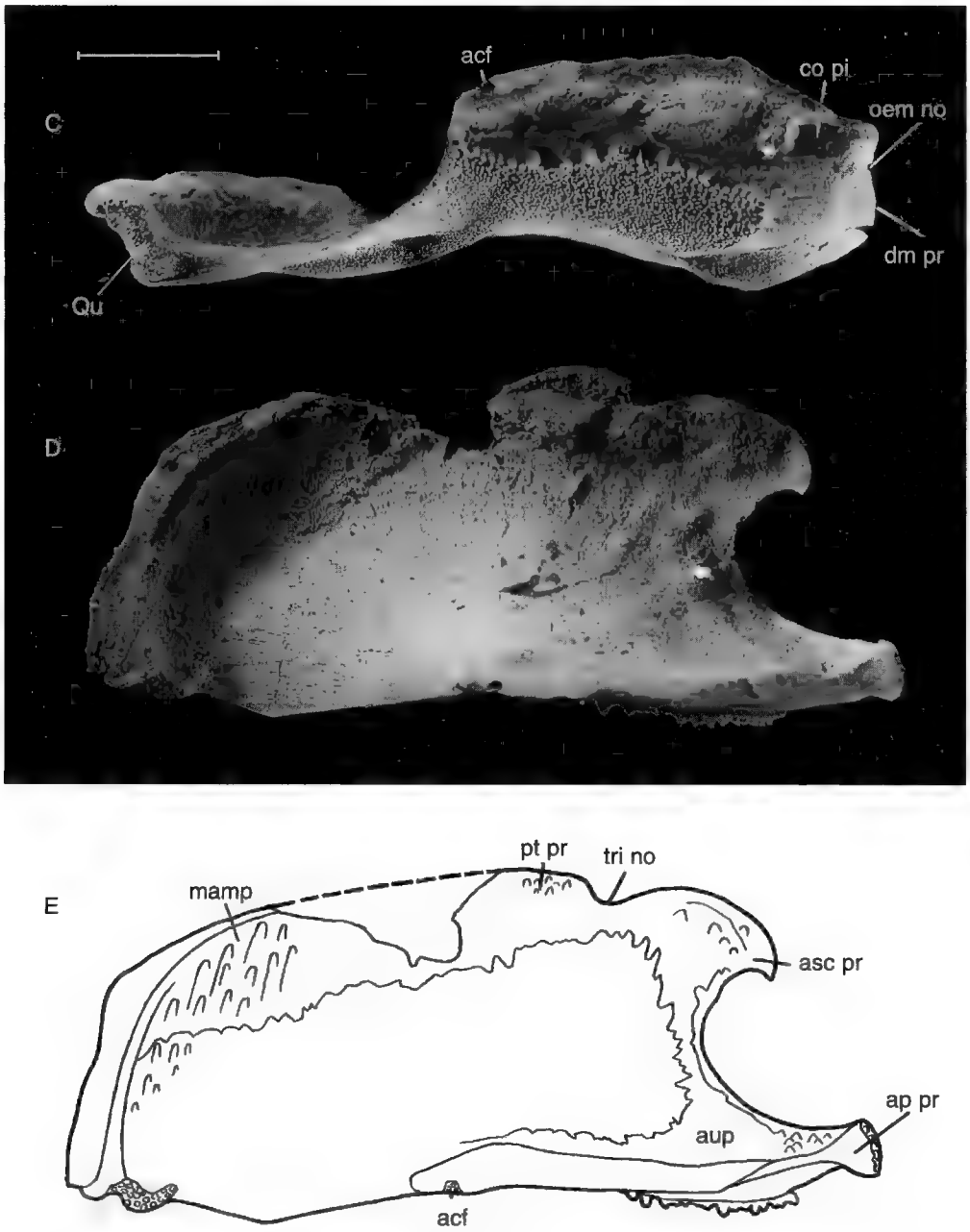

FIG. 9C-E. — *Medoevia lata* n. g., n. sp., palatoquadrate complex. C, ventral view; D, E, lateral view. Scale bar: 10 mm.
Medoevia lata *n. g., n. sp., complexe palatocarré. C, vue ventrale; D, E, vue latérale. Échelle: 10 mm.*

The sutures of the pars autopalatinum (aup) with the entopterygoid can easily be traced in the area posterior to the apical (ap pr) and dorsomedial (dm pr) processes (Fig. 9B, E). Laterally (Fig. 9C), on the horizontal plate, the suture passes near the edge of the coronoid fang pit (co pi) of the autopalatine, then towards the posteromedial edge of the overlying dermopalatine, where it becomes hidden by the overlying ventrolateral margin of the entopterygoid. Dorsally, the suture lines the basal process of the palatoquadrate (bpr) posteriorly. The suture between the autopalatine and the metapterygoid (mp) is not clearly visible. The suture between the metapterygoid and entopterygoid appears above the basal process, strongly bends anteriorly and then backwards along the dorsal margin of the palatoquadrate complex, gradually becoming indistinguishable posteriorly. The suture between the quadrate (qu) and the entopterygoid follows the posterior margin of the latter, but becomes indistinguishable dorsally, and its relationship with the posterior end of the metapterygoid is not clear. The lateral side of the palatoquadrate complex (Fig. 9D, E) clearly shows the suture between the entopterygoid, metapterygoid and autopalatine; the dermal component clearly overlies the endochondral ones, since the sutures on the surface are strongly displaced towards the centre of the complex, relatively to their position on the medial surface.

The apical process of the autopalatine part (Fig. 9C, E) is only slightly separated from the dorsomedial one by a small, yet distinct, groove probably for the passage of a branch of the palatine artery. The notch for the oblique eye muscles (oem no) in *Medoevia* is, in contrast to *Eusthenopteron*, very shallow, although it participates in the formation of the foramen, together with the ethmoid. A shallow notch limits the anteromedial ethmoidal articulation facet laterally, forming the wall of its buttress. This notch formes the medial wall of the orbitonasal canal. The horizontal plate of the autopalatine, on which rest the palatine and ectopterygoid, consists of two areas: the medial one faces ventrally and bears two pits accommodating the coronoid fangs of the lower jaw and forms two pockets under the entopterygoid for the medial processes of the palatine and the ectopterygoid. The main part of this surface is uneven and rugose. Another area is much narrower and shorter, and extends between the anterior pit for the coronoid fang to the posterior pit (Fig. 9C-E). The surface of this area is densely ornamented with a network of the vascular grooves, probably for banches of the r. maxillaris. The posterior part of this edge is sharpened and bears a patch of unfinished bone, facing the maxilla. This area probably served as an auxiliary connecting point (acf) with the maxilla beyond its contact with the palatine and ectopterygoid.

The anteromedial ethmoidal articulation area of the palatoquadrate is situated at the anterolateral corner of its autopalatine part, and on the posteromedial margin of the choana.

The dorsomedial process (dm pr) is a hemisphaerical plate of the autopalatine (Fig. 10C). Its surface is smooth and bears tiny pores. The dorsal edge of the medial margin of the horizontal plate of the palatoquadrate shows a sharp crest which reaches the basal process and served for the attachment to the suspending crest of the ethmosphenoid, by the means of a ligament. The basal process (b pr) consists of the two adjacent facets, partly separated by a pit situated just ahead of the anterior margin of the dentigerous plate of the entopterygoid.

This pit faces the crest in front of the muscle scar for the attachment of the subcephalic muscle on the basisphenoid. A similar pit is situated immediately above the dorsal facet of the

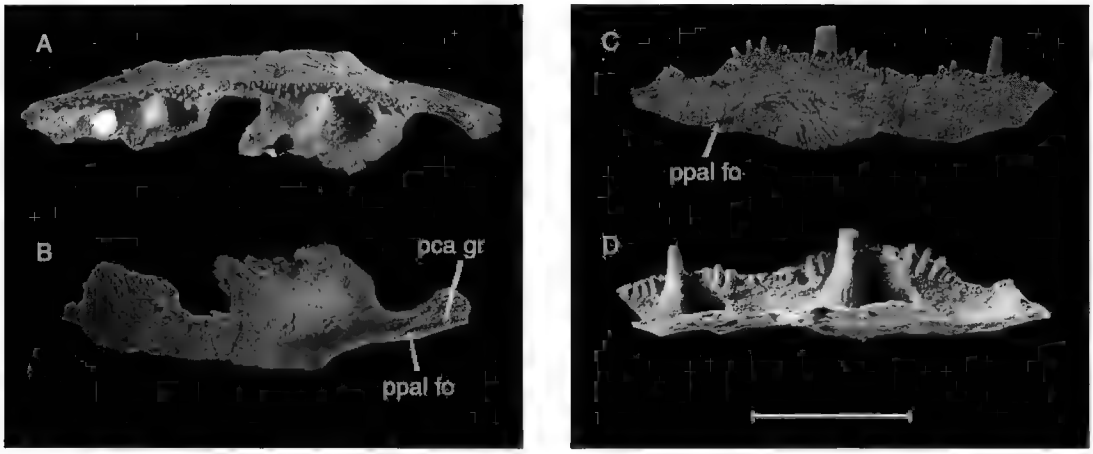

FIG. 10. — *Medoevia lata* n. g., n. sp., dermopalatine and ectopterygoid. A, ventral view; B, dorsal view; C, lateral view; D, medial view. Scale bar: 10 mm.

Medoevia lata *n. g., n. sp., dermopalatin et ectoptérygoïde. A, vue ventrale ; B, vue dorsale ; C, vue latérale ; D, vue médiale view. Échelle : 10 mm.*

basal articulation and faces the edge of the dorsal slope of the basipterygoid buttress on the basisphenoid.

The ascending process of the palatoquadrate complex (asc pr) overhangs the facet of the basal articulation and is much produced forwardly; its dorsal margin is a facet for the suprapterygoid articulation, which is devoid of periosteal layer and was probably connected to the suprapterygoid process by means of a ligament. The anteriormost part of the ascending process is beak-shaped. Its surface is smooth and abuts against the slight oblique crest on the surface of the laterosphenoid, above the foramen for the optic nerve.

The dorsal margin of the ascending process is slightly swollen, and bounds off the anterior part of the trigeminal notch (tri no), which is rather small. In *Eusthenopteron* the posterior part of this process reaches the otico-occipital block of the endocranium. In *Medoevia*, on the contrary, the trigeminal notch is situated as in *Osteolepis*, opposite the intracranial gap, so that the anterior otic connection is formed by the paratemporal process (pt pr). The lateral surface of the paratemporal process is rugose, and, although it does not clearly reach the dermal skull roof, there could exist a ligament connection with a knob on the anterior margin of the ventral surface of the supratemporal.

The dorsomedial margin of the palatoquadrate is thickened and strongly bent medially, the quadrate articulation being finally inclined by 45° relatively to the long axis of the skull. The posterodorsal surface of the palatoquadrate bears a long, deep furrow along its contact with the entopterygoid. The bottom of this structure referred to by JARVIK (1954) as the spiraculo-hyomandibular recess (sh re) is folded posteriorly; this portion housed the ventral edge of the hyomandibular.

There is a prominent oblique ridge beginning close to the posterior end of the ectopterygoid and extending postero-dorsally. Ventrally to the spiracular slit, it reaches the dorsal margin of the entopterygoid, and then forms posteriorly a recess between it and the main part of the palatoquadrate plate. This shelf is least pronounced opposite the beginning of the folding of the spiraculo-hyomandibular groove. A this level, the shagreen field of the entopterygoid forms a posteriorly directed tongue. Ventrally to this tongue, there is an articulation facet with an unfinished periosteal surface. The role of this facet is unknown.

The lateral surface of the palatoquadrate complex bears numerous muscle scars (Fig. 9D, E). The most conspicuous of them is a rugose field in the posterodorsal part, which could represent the insertion area for the posterior portion of the m. adductor mandibulae (mamp). This area begins opposite the lateral commissure and occupies a deep depression, formed by the entopterygoid and the laterally turned quadrate part. The dorsal surface of the autopalatine part bears a rough superficial ornamentation suggestive of a muscle insertion; a strong ridge, running along the edge of the embayment below the ascending process, may also correspond to a muscle insertion. The lateral surface of the ascending process also bears ridges and uneven tubercles, characteristic for areas of muscle attachment. The latter may have housed the insertion of the anterior portion of the m. adductor mandibulae. Alternatively, it may have been for the medial portion of this muscle, while the ridge just mentioned served as the attachment of its anterior portion. The rugose area on the dorsal surface of the autopalatine part more probably served the insertion of the principal portion of the m. levator bulbi.

Lower jaw

No suture between the external dermal bones of the lower jaw is visible in *Medoevia*, apart from a short trace posteriorly, between the dentary and the suprangular (Fig. 11A). The pores of the sensory canal are numerous and scattered over the ventral half of its lateral surface. The only visible pit-line is that situated on the suprangular. The length of the adductor fossa (ad fo) represents one third of the total length of the jaw.

A pair of the anterior teeth in the dentary tooth row is about twice as large as the others (Fig. 11B, C). Posteriorly, the tooth row ends in the anterior third of the adductor fossa. Posteromedially to the dentary part of the symphysis arises a buttress which is formed by the Meckelian bone (mentomandibular, mm). Its medial part is not fully ossified and a perichondral surface faces a similar one in the opposite lower jaw ramus. The perichondral surface is prolonged posteroventrally to form a small patch at the base of the buttress, immediately above the anterior opening for the mandibular sensory line canal, but its function is unknown. A deep pit is situated dorsolaterally to it and is interpreted by Jessen (1966) as the area for the insertion of the m. geniohyoideus (mgh pi). The buttress is capped with a rectangular, shagreen-covered adsymphysial plate (ads), which meets posteriorly the vertical lamina of the anterior coronoid. The teeth on the top of the vertical laminae of all the three coronoids are disposed in several rows, the largest being situated close to the fangs, and those parts of the laminae which support the fangs laterally are prominently raised above the level of the dentigerous edge of the dentary. The anterior coronoid is the largest, and the posterior one is the smallest of all three, its fang being half the size of that on the precoronoid. The floor of the coronoid fossae is made up by a thin lamina formed by the Meckelian bone.

The praearticular anterior process (pra pr) contacts the posterior medial process of the splenial opposite the anterior fang of the first coronoid. The suture here is much obliterated but still visible. Its lateral margin, where it is fused with the coronoids, is sinusoidal. The medial margin is straight, and one can clearly see the contact with the Meckelian bone, which connects the praearticular with the lower margin of the jaw, composed by the infradentaries.

Posteriorly the praearticular extends as far as the middle of the lower jaw articulation, the shagreen of minute teeth being gradually replaced by small pits and a network of shallow crests. A well pronounced ridge runs along the posterior end of the bone, parallel to the edge of the adductor fossa. A strip of its ventral surface is devoid of ornamentation.

The praearticular canal for the chorda tympani starts with a large foramen (pra fo) in the posteroventral edge of the bone and runs forward, piercing the medial wall of the adductor

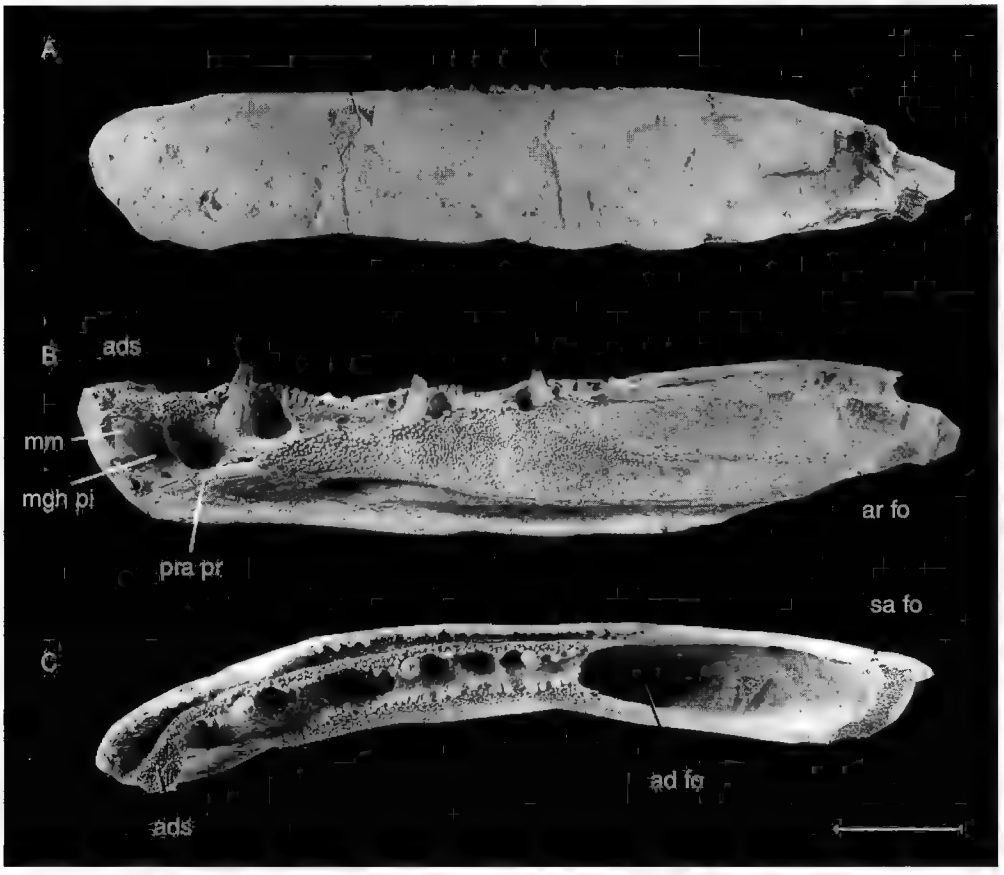

FIG. 11. — *Medoevia lata* n. g., n. sp., lower jaw. A, lateral view; B, medial view; C, dorsal view. Scale bar: 10 mm.
Medoevia lata *n. g., n. sp., mâchoire inférieure. A, vue latérale; B, vue médiale; C, vue dorsale. Échelle: 10 mm.*

fossa. Further anteriorly, it is represented by a groove. The largest Meckelian fenestra is situated opposite the first coronoid fossa, and the next two much smaller fenestrae are opposite the second coronoid pit and the front of the adductor fossa.

A foramen situated ventrally to the posterior opening of the prearticular canal may represent the opening of the articular canal (ar fo). Patches of incompletely ossified bone with a perichondral lining are situated anteriorly and posteriorly to it, and connected with the posterior surface of the articular. These structures may serve the connection with the 'tongue-like' process of ceratohyal 2 (JARVIK, 1980). The dorsal opening of the supra-angular canal (sa fo) enters the jaw right above the mandibular joint. There are two openings in the adductor fossa on the anterolateral edge of the articular: a larger one ventrally and a smaller one dorsally, both probably serving as outlets of the supra-angular canal.

The posterodorsal edge of the dentary and the supra-angular are devoid of cosmine covering, since this area was covered by the ventral lamina of the quadratojugal. This area extends as far back as the posterior end of the mandibular articulation. Ventrally, the supra-angular shows a short, but deep notch laterally to the articulation surface for the ceratohyal 2.

OPERCULO-SUBMANDIBULAR SERIES AND GULAR

The opercular in *Medoevia* is almost twice as large as the subopercular (Fig. 12A-D). It is about 1.3 times longer than deep. Its anterodorsal margin forms a depressed contact area, devoid of cosmine, for the lateral extrascapular (exl ar). The anterior margin exhibits a narrow, slightly curved overlap surface for the preopercular. The rugose articulation facet for the contact with the opercular process of the hyomandibula (hy ar) is situated at the anterodorsal corner, close to the anterior margin of the bone. The subopercular is much lower than in eusthenopterids (JARVIK, 1944a, 1952; VOROBYEVA, 1977a). Its overlap surface with the opercular is only slightly curved. The anterior margin projects medially and its ventral part is slightly embayed for the contact with the posterior end of the lower jaw. The pit for the contact with the lateral process of ceratohyal 2 is accompanied by a rugose area anteriorly (epch2 ar), which is situated within the dorsal half of the bone, close to its anterior margin.

The median gular in *Medoevia* (Fig. 13A, B) is rounded in shape. Its lateral parts contacted the anterior infradental flanges of the lower jaw. There is a well-marked, curved pit-line on the ventral surface of this bone. The lateral gulars (Fig. 13 C, D) are rather broad and short, their length being only about 2.5 times more than their maximum width. The pit-line is situated in the anterior third of the bone. The median gular overlaps the corresponding surfaces which are devoid of cosmine on the anteromedial margins of the lateral ones. The left lateral gular slightly overlaps the right one to close the slit between them; there is a corresponding cosmine-covered depressed area along the medial margin of the right lateral gular. The posterior edge of the bone is rounded and almost transversal in position. Its dorsal surface is covered by a network of vascular grooves.

The submandibulo-branchiostegal (Fig. 14A, B) is roughly oval in shape and shows two surfaces separated by a sharp ridge anteriorly. Its lateral lamina is only partly cosmine-covered. The anterior edge of the overlapped surface shows a small notch for the contact with the posterior end of the lower jaw (lj no).

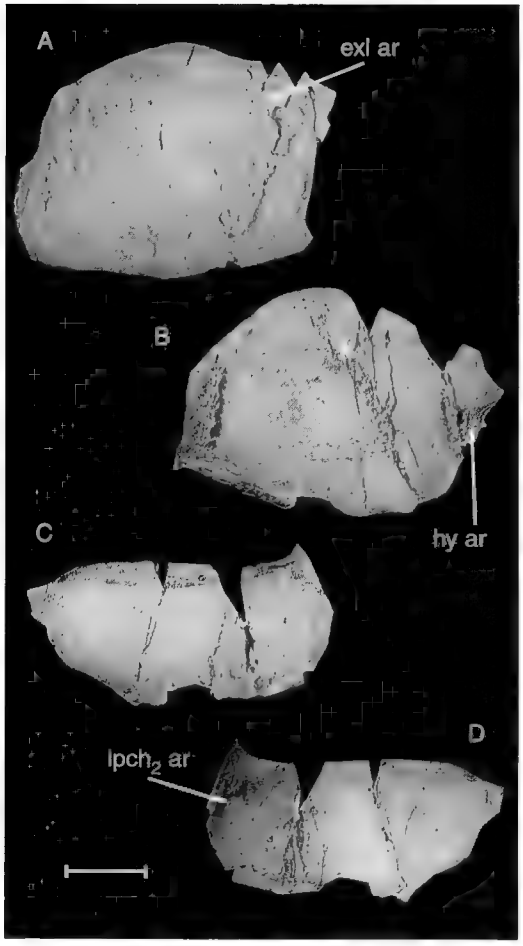

FIG. 12. — *Medoevia lata* n. g., n. sp. A, B, opercular; C, D, subopercular; A, C, lateral view; B, D, medial view. Scale bar: 10 mm.

Medoevia lata *n. g., n. sp. A, B, operculaire ; C, D, sous-operculaire. A, C, vue latérale ; B, D, vue médiale. Échelle : 10 mm.*

There are five submandibulars (Fig. 14C-J), the anterior one extending slightly in front of the level of the posterior end of the median gular. The size of the plates is not equal on either sides. For example, the left submandibular 5 is almost 1.5 times longer than the corresponding element on the right side. The pit-line of the submandibular 7 almost crosses the bone transversally.

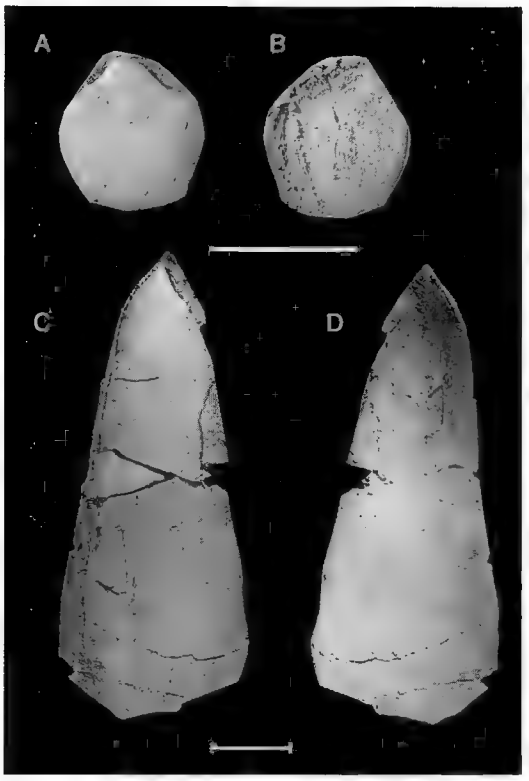

FIG. 13. — *Medoevia lata* n. g., n. sp. A, B, median gular; C, D, lateral gular. A, C, ventral view; B, D, dorsal view. Scale bar: 10 mm.

Medoevia lata *n. g., n. sp. A, B, gulaire médiane; C, D, gulaire latérale; A, C, vue ventrale; B, D, vue dorsale. Échelle: 10 mm.*

DENTAL PLATES OF THE MOUTH CAVITY AND PHARYNX

About five hundred dental plates of various size and shape are present in the material (Fig. 15A-G). Due to the compression of the head during fossilization, and to the chemical preparation of the specimen, almost all of them became detached, so that only the paraotical plates (Fig. 15A, B) can be identified readily, since they are the largest ones. These are almost flat and pentagonal in shape. Their ventral surface bears simple, short and blunt denticles, the dorsal surface being uneven and covered by numerous, small nutrient foramina. The size of the others varies from 0.8 mm to several millimeters in diameter. Their outlines differ from rounded or oval to polygonal or irregular, a diamond-shaped type with a thick base being common. There are four major types of denticulation:

1 – short and blunt denticles, either with a single apex or multicuspid (Fig. 15F);
2 – conical ones of various length, inclined in one direction relatively to the basal plate;

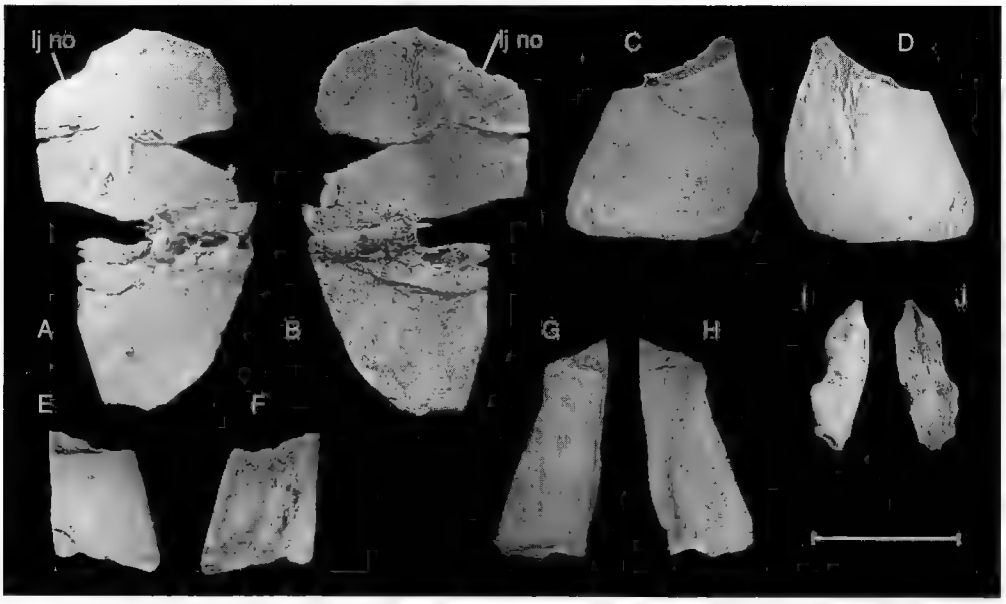

FIG. 14. — *Medoevia lata* n. g., n. sp., bones of the submandibular series. A, B, submandibulo-branchiostegal plate; C, D, submandibular 7; E, F, submandibular 6; G, H, left submandibular 5; I, J, submandibular 4; A, C, E, G, I, ventral view; B, D, F, H, J, dorsal view. Scale bar: 10 mm.

Medoevia lata *n. g., n. sp., os de la série submandibulaire. A, B, plaque submandibulo-branchiostégale ; C, D, submandibulaire 7 ; E, F, submandibulaire 6 ; G, H, submandibulaire 5 gauche : I, J, submandibulaire 4. A, C, E, G, I, vue ventrale ; B, D, F, H, J, vue dorsale. Échelle : 10 mm.*

3 – transitional types between the first two (Fig. 15C-E);

4 – tiny cones forming a row along the edge of a pit in the middle of an otherwise smooth plate; which resemble in position the denticles described below on the anocleithrum, cleithrum and clavicle (Fig. 15G).

HYOID ARCH

The hyomandibula of osteolepiforms is known in *Eusthenopteron foordi* (WESTOLL, 1943; JARVIK, 1954, 1980; SMITHSON & THOMSON, 1982), *Megalichthys* (WATSON, 1926; ROMER, 1941), *Osteolepis* (THOMSON, 1965), *Jarvikina wenjukowi* and *Thursius estonicus* (VOROBYEVA, 1977a).

The general shape of the hyomandibula in *Medoevia* (Fig. 16A, B) does not differ significantly from that in *Eusthenopteron*, being slightly deeper, the distal end being broader and shorter and the angle of the postero-dorsal edge being more acute than in the latter. The opercular articulation area (op ar) is a triangular depression devoid of periostal cover and situated on the lateral surface of the bone. This corresponds to the opercular process, but it is evident that the process itself was composed of cartilage. The laterally directed ridge, which forms a pocket for

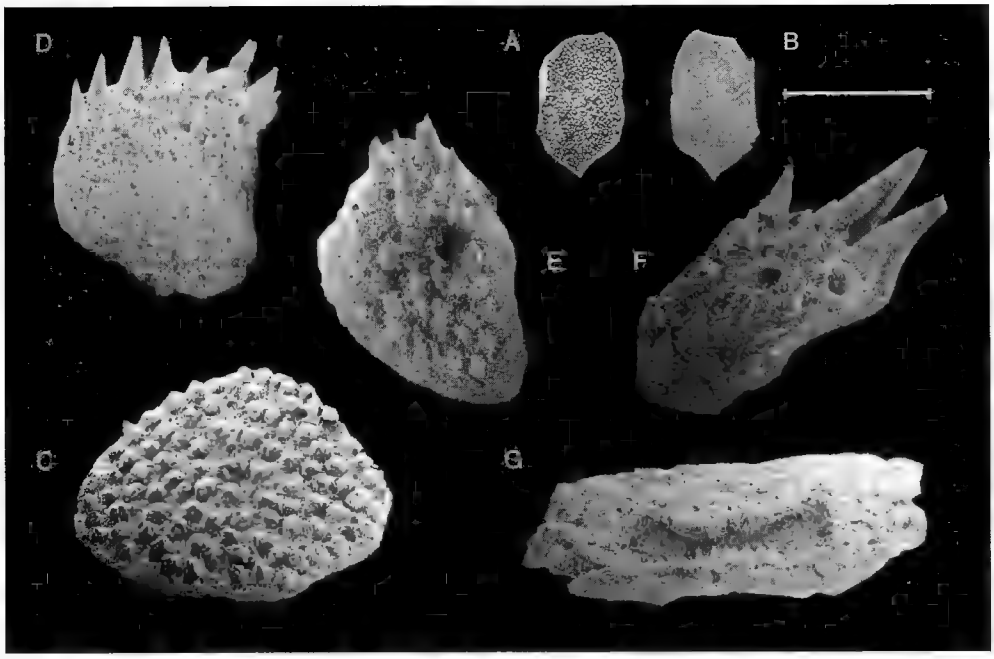

FIG. 15. — *Medoevia lata* n. g., n. sp., dental plates of the mouth cavity and pharynx. A, B, paraotical plate. A, ventral view; B, dorsal view. C, D, scale bar: 2.2 mm; E, G, scale bar: 3 mm; F, scale bar: 3.2 mm.

Medoevia lata *n. g., n. sp., plaques dentées de la bouche et du pharynx. A, B, plaque paraotique ; A, vue ventrale ; B, vue dorsale ; C, D, échelle : 2,2 mm ; E, G, échelle : 3 mm ; F, échelle : 3,2 mm.*

the insertion of the m. protractor hyomandibularis (prhy) is distal to the opercular process, thus the position of the insertion of this muscle is displaced distally in comparison to its position in *Eusthenopteron*. Distally, and very close ventrally to it, there is another rounded muscle scar of unknown nature. The ridge for the insertion of the m. adductor hyomandibularis (ahy ri) is situated exactly in the same position as in *Eusthenopteron*. The proximal surface of the medial side bears a groove with rugose walls nearly to the middle of the bone. A wide groove with a similar ornamentation is found on the medial side of the bone, dorsally to the ridge for the attachment of the m. adductor hyomandibularis and obviously represents an impression of the jugular vein (juv). The most proximal evidence for the r. hyomandibularis is the orifice of the hyomandibular canal (hyc) which pierces the bone and appears on the lateral side shortly before the level of the anterior margin of the notch for the opercular process, then passing distally. The wall of the canal is pierced medially by a small foramen for the r. opercularis VII (ro VII fo).

The groove for the r. hyoideus (rhy gr) is observed proximally at the dorsal edge of the bone; thus, the branching of the truncus hyomandibularis occurred more proximally and left no traces on its surface. The groove for the r. hyoideus extends to the base of the opercular process and it is impossible to trace it more distally. The articulation facet for the stylohyal (sty ar) is small and situated at the very tip of the distal process, being displaced medially.

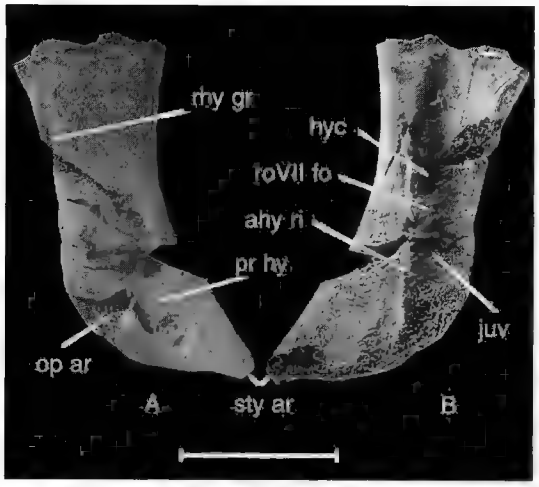

FIG. 16. — *Medoevia lata* n. g., n. sp., hyomandibula. A, lateral view; B, medial view. Scale bar: 10 mm.

Medoevia lata *n. g., n. sp., hyomandibulaire. A, vue latérale; B, vue médiale. Échelle: 10 mm.*

The stylohyal was probably not ossified. As in *Eusthenopteron*, the ceratohyal consists of two elements: the ceratohyal 1 (ch1) and ceratohyal 2 (ch2). The posterior element, or ceratohyal 1 (Fig. 17C-F), is a rather short rod of complicated construction. A wide and deep oblique groove crosses its dorsolateral surface, and it bears four articulation facets: distal, proximal, ventral and lateral. The lateral and ventral facets are accompanied by pits, which lie proximally to them in both cases. The lateral facet (sop f) might serve the articulation with the suboperculum and the ventral one (smb f) connects the bone with the submandibulo-branchiostegal plate. The ceratohyal 2 (Fig. 17A, B) is a large plate-like bone, characterized by an almost straight anterior margin and a crescent-shaped posterior one. Its anterior edge bears a pronounced groove for the anterior continuation of the efferent artery of the first branchial unit (ea1 gr). The dorsal surface bears a network of vascular grooves, which branch off from a notch in the proximoventral corner. The hypohyal (Fig. 17G, H) is a massive triangular bone, with a curved groove for the anterior portion of the efferent artery (ea1 gr). Its lateral surface is rugose and served the attachment of the anterior end of the interarcual ligament.

THE BASIBRANCHIAL SERIES AND BRANCHIAL ARCHES

The elements of the basibranchial series and the branchial arches are described in *Eusthenopteron foordi* and *Glyptolepis groenlandica* (JARVIK, 1954, 1962, 1963, 1972, 1980). It is described here for the first time in an osteolepidid.

The basibranchial series consists of the two elements (Fig. 18A, B; bb1, 2), basibranchial 1 and basibranchial 2. The foremost element, or basibranchial 1 is a massive heptagonal bone with two articulation facets on each side, for the hypobranchials 1 and 2, a pair of facets on the anterior margin for the hypohyals, a median facet posteriorly for the basibranchial 2, and a paired area devoid of the periosteal lining, close to the anterior margin of the ventral side, for the ligamentous or cartilaginous attachment of the urohyal (uh ar). The posterior part of its

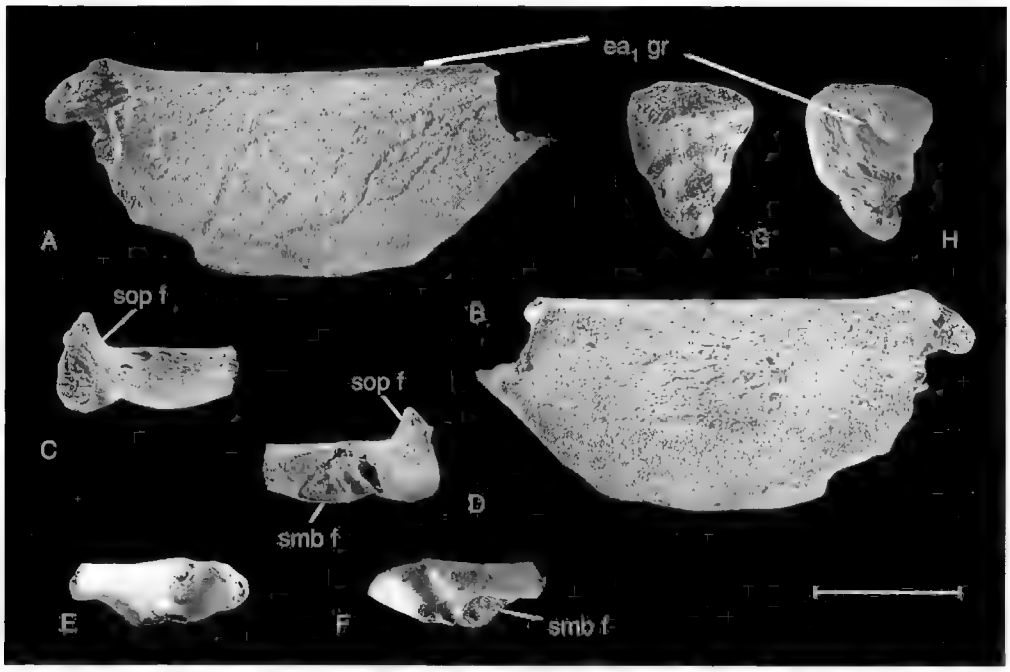

FIG. 17. — *Medoevia lata* n. g., n. sp., elements of the hyoid arch. A, B, ceratohyal 2; C-F, ceratohyal 1; G, H, hypohyal. A, G, posterior view; B, H, anterior view; C, medial view; D, lateral view; E, ventral view; F, dorsal view. Scale bar: 10 mm

Medoevia lata *n. g., n. sp., éléments de l'arc hyoïdien. A, B, cératohyal 2 ; C-F, cératohyal 1 ; G, H, hypohyal. A, G, vue postérieure ; B, H, vue antérieure ; C, vue médiale ; D, vue latérale ; E, vue ventrale ; F, vue dorsale. Échelle : 10 mm.*

ventral surface bears a deep, anterodorsally directed pocket; its bottom is rugose and bears several vascular, possibly nutrient foramina; this pocket may have served for the insertion of the paired aponeuroses of m. sternohyoideus (mshy). The transverse crest, which bounds off the pocket anteroventrally, extends between the articulation surfaces of the first pair of hypobranchials; its edge is devoid of periosteal lining, thereby suggesting that it is a trace of the limit between the anterior and the posterior components (basihyal + basibranchial proper) of the bone. Its dorsal surface is rugose and obviously supported the denticulated plates of the mouth cavity. The second basibranchial element is a short, horseshoe-shaped element, that was connected to the posterior articulation surface of basibranchial 1. Its ventral notch accommodated the ascending plate of the urohyal. The posterior surface shows a pair of articulation facets for the hypobranchials of the third branchial arch.

A very poorly preserved sublingual rod (Fig. 18A; sr) is present. It is triangular in cross-section and very lightly ossified, possessing no periosteal lining over its dorsal ridge. Anteriorly, its dorsal ridge becomes higher and its basal part narrower.

The general shape of the urohyal (Fig. 19A, B) is similar to that in *Eusthenopteron* (JARVIK, 1954, 1980), though more elongated in shape. The anterior part of its dorsal edge is a sharp

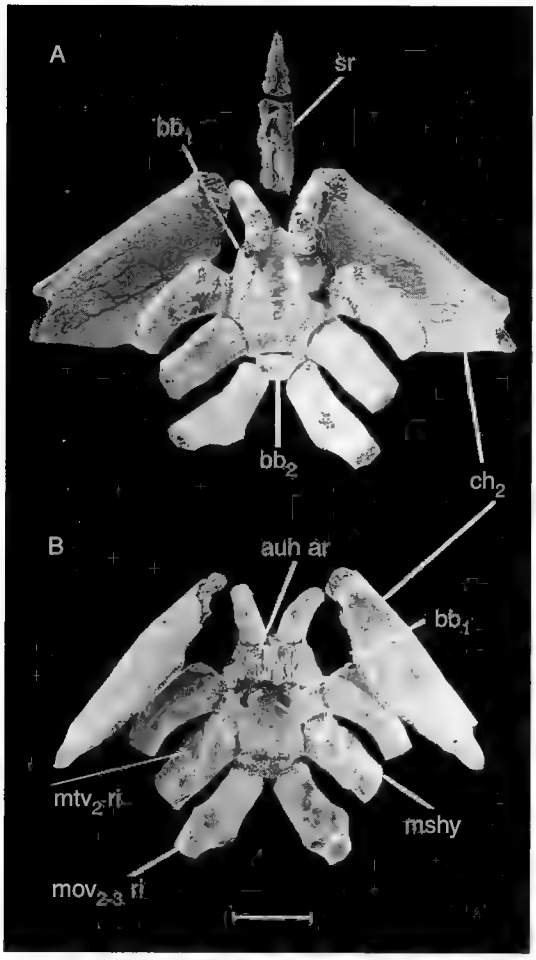

FIG. 18. — *Medoevia lata* n. g., n. sp., mounted elements of the hyoid and branchial arches. A, dorsal view; B, ventral view. Scale bar: 10 mm.

Medoevia lata *n. g., n. sp., arcs hyoïdiens et branchiaux montés. A, vue dorsale; B, vue ventrale. Échelle : 10 mm.*

crest, interrupted by two poorly ossified areas, where it touched the transversal ridges of the ventral side of the basibranchial 1. Posteriorly, the edge becomes blunt until the posterior end of the bone. The posteroventral corner of the bone bears a small notch. Its ventral surface is flat and striated, probably due to the attachment of a ligament. The characteristic feature of its lateral surfaces is an oblique, anteroventrally directed ridge, ventrally to which the surface of the bone is rugose. This rugose surface may have served the attachment of m. rectus cervicis (rece). The tubercle in the middle of the ventral edge could have been the attachment of m. geniohyoideus (ghy tu).

The hypobranchials 1-3 are rather uniformly built and differ by the arrangement of the grooves, tubercles and ridges (Figs. 18A, B, 19C-F). The most conspicuous feature of the ventral surface of hypobranchial 1 is a longitudinal groove, which probably housed the afferent artery

of the first branchial unit (aa1 gr). Proximally, there are two tubercles on either sides of this groove. The proximal part of the dorsal surface of this bone shows a slight rugosity and two patches devoid or periosteal lining, which might represent the attachment area for the interarcual ligament (ial tu). The dorsal surface of hypobranchial 2 bears only a massive, oblique rostro-caudal ridge, followed by a smaller ridge and a pit in front of its posterior portion for the mm. transversalis ventralis 2 (mtv2 ri) and obliquus ventralis 2 (mov2 ri). A small tubercle lacking periosteal lining is situated in the middle of the anterior edge of the bone, opposite a similar structure in the posterodorsal area of the hypohial 1. The dorsal surface of the hypobranchial 3 (Fig. 19E, F) is smooth, but the ventral one presents three tubercles in the middle of the bone, connected to each other by a distinct ridge. The anterior tubercle is the largest, and the smallest one is located posteriorly to it; this pair constitutes the anterior margin of a deep pit. The third tubercle is more like a short process; it is abutted by a short ridge anteriorly and limits another pit on the posterior side of the bone. It is likely that the largest tubercle served, as in *Glyptolepis groenlandica* (JARVIK, 1962, 1963, 1972, 1980), the articulation of hypobranchial 4 (hby ar). The smaller tubercles seem to have served the attachment of the m. obliquus ventralis 3 (mov3 tu).

POSTCRANIAL SKELETON

The dorsal bones of the shoulder girdle (post-temporal, supracleithrum and anocleithrum) are described only in a few osteolepiform fishes, such as *Eusthenopteron* (JARVIK, 1944b, 1980), *Osteolepis* (JARVIK, 1948) and *Canowindra* (LONG, 1985c).

The post-temporal in *Medoevia* (Fig. 20A, B) is a convex, rectangular bone. Its anterior overlapped surface is not preserved on either sides, so that the mode of articulation with the extrascapulars is not clear. The lateral (opercular) process (op pr) is much larger than in *Eusthenopteron*. The supracleithrum (Fig. 20C, D) is about half the size of the post-temporal. Anteriorly it bears a long triangular process, medially to the anterior opening of the main lateral line sensory canal, for the contact with the post-temporal. Its lateral portion overlapped by the opercular (op pr) is also broad. A short, oblique pit-line is situated close to the anterior edge of the non-overlapped surface.

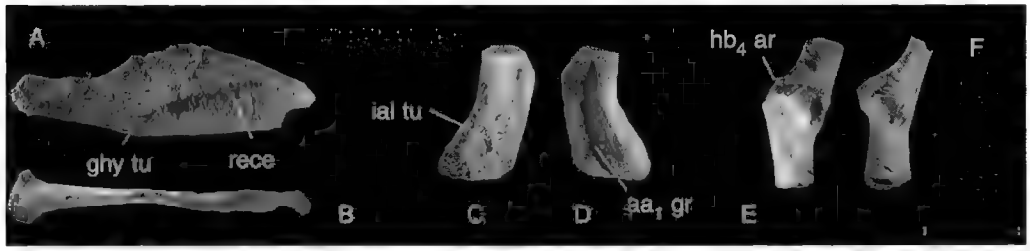

FIG. 19. — *Medoevia lata* n. g., n. sp. A, B, urohyal; C, D, hypobranchial 1; E, F, hypobranchial 3. A, lateral view; B, E, dorsal view; C, ventral view; E, ventromedial view; F, dorsolateral view. Scale bar: 10 mm.

Medoevia lata *n. g., n. sp. A, B, urohyal; C, D, hypobranchial 1; E, F, hypobranchial 3. A, vue latérale; B, E, vue dorso-latérale; C, vue ventrale; E, vue médioventrale; F, vue dorsolatérale. Échelle: 10 mm.*

The anocleithrum in *Medoevia* (Fig. 20E, F) differs significantly in shape from that of *Eusthenopteron* and is closer to that of *Canowindra* (LONG, 1985c). The anocleithral process (ano pr) is very well developed, its length being half of the total bone length, and the angle it forms with the main plate is about 90°. Its medial side bears a long, massive ridge, which runs towards the apex of the process. The process for the articulation with the supracleithrum (sc pr) is large and rather elongated in shape. Laterally, the cosmine layer is resorbed and replaced by scarce, bi- or tricuspidate denticles on bony tubercles. The cleithrum in *Medoevia* (Fig. 21A-C) has the typical overall shape for osteolepiforms, but some of its features are peculiar. The ventral and dorsal laminae are approximately equal in length, forming between them an angle of about 140°. The cosmine cover is practically absent, except on a patch posteriorly in the central part of the bone (Fig. 21A). The rest of the external dermal ornament is a network of high ridges bounding off deep pits. The tops of the ridges bear one row of bi- or tricuspidate, caudally directed denticles, like those on the anocleithrum. A deep and narrow area, between the main ornamented surface and the overlap area for the opercular and subopercular bears minute pits and tubercles, the latter being capped with the same type of denticles, with 5-7 cusps, like on the posterior surface of the bone.

The process of the cleithrum is only insignificantly developed because the external area overlapped by the clavicle (clav ar) is extremely small, as in *Megalichthys hibberti* (ANDREWS & WESTOLL, 1970b) and the "osteolepid B" from the Upper Devonian of Armutgözlek Tepe, Turkey (JANVIER & MARCOUX, 1976; JANVIER, 1980). The breadth of the inwardly bent area overlapped by the operculum and suboperculum (mem ar) is similar to that in *Osteolepis macrolepidotus* (JARVIK, 1948). Judging from the structure of the antero-medial margin of the cleithrum, this bone never reached the interclavicle. The medial surface of the dorsal part of the cleithrum (Fig. 21B) shows a prominent ridge on its anterior edge, formed by the anterior lamina. It is bordered posteriorly by a groove receiving the anocleithral process (ano pr gr). A shallow, depressed area situated posteriorly (pano pr ar) receives the large posterior process of the anocleithrum. There is a well-marked groove for the overlap of the vertical process of the clavicle ventrally. It begins on the lateral surface, then extends along the anterior edge of the cleithrum, and passes to the medial surface up to the ventral buttress of the scapulocoracoid.

The clavicle is completely devoid of cosmine (Fig. 22D, E). The two clavicles are only partly preserved but allow a recontruction of the bone. The ornamentation of their ventral surface consists of pits, the largest of them being situated proximally. Smaller pits are distributed along the margins of the ventral lamina, its centre being smooth with the exception of small nutrient foramina. The edges of the large pits are provided with medially directed dentine denticles, the dorsolateral lamina bears the same type separate multicuspidate denticles as the cleithrum. The medial edge of the dorsal side of the ventral lamina bears a clearly defined overlap surface for the interclavicle (icl ar), which is devoid of the slight radial ridges, that are seen over the rest of the surface. The posteromedial edge of the ventral lamina is depressed. It runs posteriorly to form a groove, bordered by a massive crest laterally. This groove housed the anteroventral process of the cleithrum. The crest runs posterodorsally on its lateral surface up to the midheight of the ascending process. The lateral surface of the ascending process bears an overlap surface, which fits the anterolateral edge of the medially reflected lamina of the cleithrum, forming the posterolateral wall of the branchial chamber. The rest of the lateral surface serves as its prolongation.

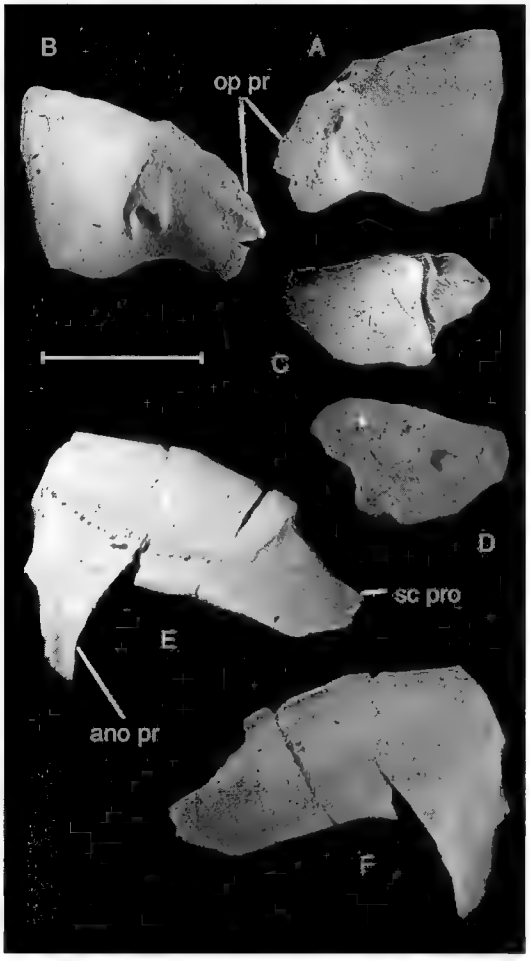

FIG. 20. — *Medoevia lata* n. g., n. sp., dorsal elements of the pectoral girdle. A, B, post-temporal; C, D, supracleithrum; E, F, anocleithrum. A, C, E; dorsal view; B, D, F, ventral view. Scale bar: 10 mm.

Medoevia lata *n. g., n. sp., éléments dorsaux de la ceinture pectorale. A, B, post-temporal; C, D, supracleithrum; E, F, anocleithrum. A, C, E, vue dorsale; B, D, F, vue ventrale. Échelle: 10 mm.*

The overlapped surface bears vertical crests for the attachment ligaments, the free surface being smooth.

The interclavicle is a thin, oval symmetrical plate, which is slightly shorter than that in *Eusthenopteron* (JARVIK, 1944b). Its dorsal surface is smooth. There is a very slight and shallow depression close to its anterior margin. The ventral surface is subdivided into two symmetrical halves by a median ridge (Fig. 22C; me ri) and, contrary to *Eusthenopteron*, the ornamentation is lacking.

ENDOSKELETAL SHOULDER GIRDLE AND PECTORAL FIN

The endoskeletal shoulder girdle in *Medoevia* agrees in general with that in *Eusthenopteron* (ANDREWS & WESTOLL, 1970a; JARVIK, 1980), *Megalichthys* (ANDREWS & WESTOLL, 1970b),

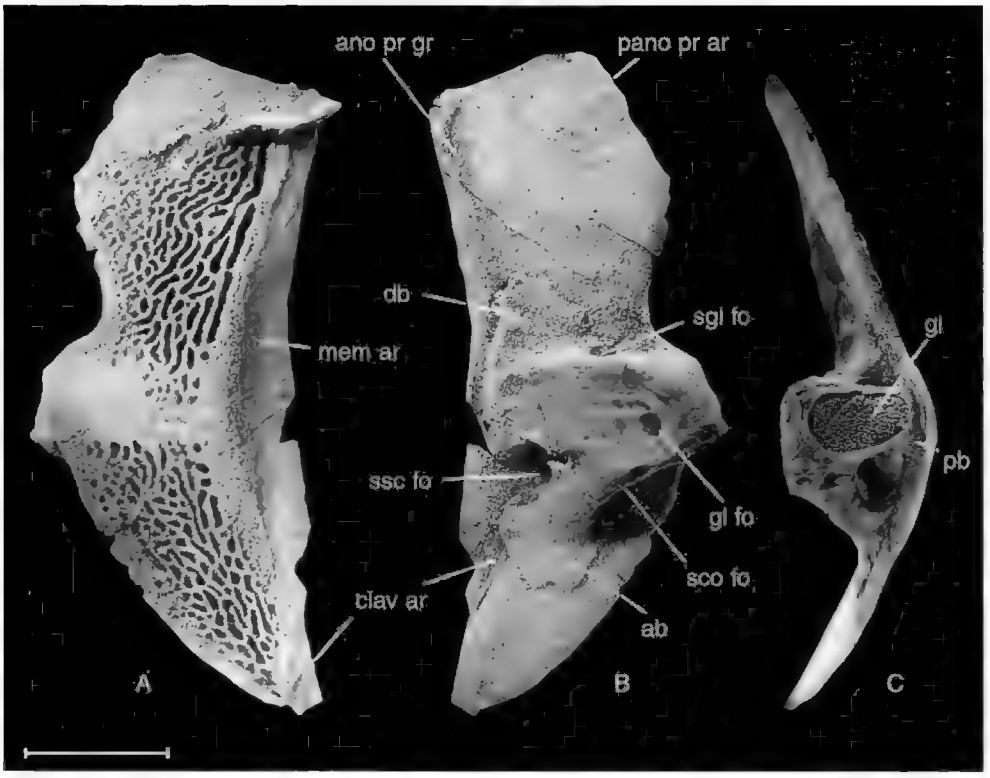

FIG. 21. — *Medoevia lata* n. g., n. sp., cleithrum and endoskeletal pectoral girdle. A, lateral view; B, medial view; C, posterior view. Scale bar: 10 mm.

Medoevia lata *n. g., n. sp., cleithrum et ceinture pectorale endosquelettique. A, vue latérale; B, vue médiale; C, vue postérieure. Échelle: 10 mm.*

Ectosteorhachis (THOMSON & RACKOFF, 1974) and the "osteolepids A and B" (JANVIER & MARCOUX, 1976; JANVIER, 1978, 1980). The foot of the dorsal buttress (db) is the largest, and has a significant dorsal extent (Fig. 21B, C). Anteriorly, it almost contacts the margin of the cleithrum. The glenoid fossa (gl) faces posteriorly. It is roughly rectangular to oval in shape, rather than pear-shaped, and its surface is screw-shaped. It is bordered by a sharp ridge of periosteal bone, probably for the connective tissues of the joint. The ventral and dorsal surfaces are separated from the medial one by sharp ridges. The glenoid foramen (gl fo) is situated in the posteroventral corner of its medial surface; it is continued internally by a short canal leading into the bone mass, and then branching and opening posteriorly on the ventral surface by two small foramina divided by a short ridge. Another longitudinal ridge divides the ventral surface into two areas and ends by a rugose area, anteriorly to the lateral foramen. A distinct muscle attachment area is situated between the dorsal edge of the glenoid fossa and the supraglenoid canal. The supra-

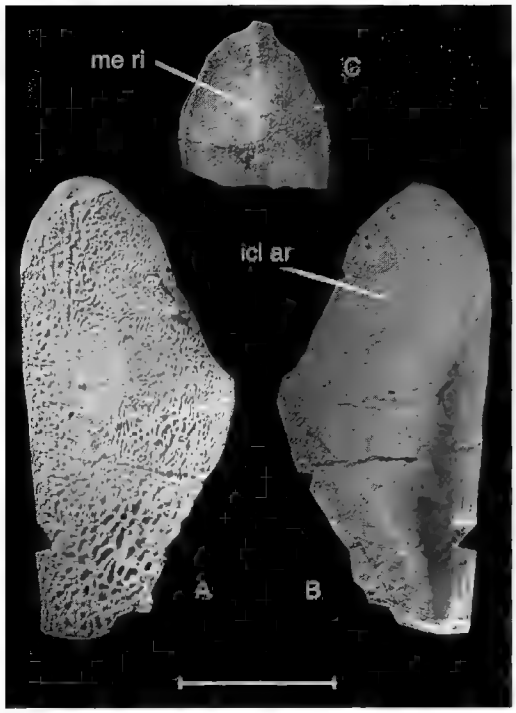

FIG. 22. — *Medoevia lata* n. g., n. sp. A, B, ventral lamina of the clavicle; C, interclavicle. A, C, ventral view; B, dorsal view. Scale bar: 10 mm.

Medoevia lata *n. g., n. sp. A, B, lame ventrale de la clavicule ; C, interclavicule. A, C, vue ventrale ; B, vue dorsale. Échelle : 10 mm.*

coracoid foramen (sco fo) is the largest, the opening of the subscapular fossa (ssc fo) is somewhat smaller and the supraglenoid foramen (sgl fo) is the smallest of all three.

The humerus (Fig. 23A-F) is incompletely preserved, its distal end, including the radial and the preaxial side of the ulnar condyle being eroded away. The humeral head (ca hu) fits well the glenoid fossa of the scapulocoracoid, being somewhat rectangular to oval and screw-shaped. The ectepicondylar ridge (ect ri) is a short crest on the distal part of the bone, and is interrupted by an eroded surface. There are two prominent ridges on the dorsal surface of the bone (Fig. 23A, D), separated by a smooth, deep, broad and regular groove. The longer ridge starts from the very edge of the humeral head in its dorsal part and runs toward the distal end of the bone. Another one runs parallel to the distal part of the posterior edge of the ectepicondylar process, then turns proximally to border the entepicondylar foramen (Fig. 23C, F).

The supinator process joins the deltoid process distally forming together a massive, rugose ridge (su + de ri). It is connected distally, as in *Eusthenopteron*, with the entepicondylar ridge by a bony bridge over the entepicondylar foramen (ent fo).

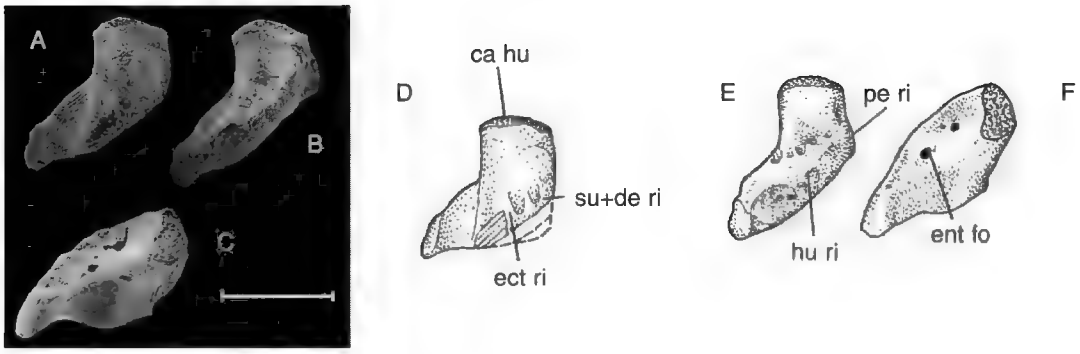

FIG. 23. — *Medoevia lata* n. g., n. sp., humerus. A, D, dorsal view; B, E, ventral view; C, F, proximo-postaxial view. Scale bar: 10 mm.

Medoevia lata *n. g., n. sp., humérus. A, D, vue dorsale ; B, E, vue ventrale ; C, F, vue proximo-postaxiale. Échelle : 10 mm.*

The humeral ridge (hu ri) is even more fluted than in *Eusthenopteron*. It is perforated by a row of five foramina of different size (Fig. 23B, E), two of them being the largest. The most postaxial one is the entepicondylar foramen, which is, unlike in *Eusthenopteron*, situated within the general row, and not separated from the others by a ridge. Proximally, the humeral ridge meets the pectoral one (pl ri), which is represented by a massive, rugose knob situated close to the anterior edge of the humeral head. Another rugose surface borders the edge between the pectoral and the deltoid ridges.

VERTEBRAE

Several elements of the anterior vertebrae are preserved in *Medoevia*, including three complete and several broken intercentra, two pleurocentra and six separate halves of the neural arches. The composition of the vertebra is as in *Osteolepis panderi* (ANDREWS & WESTOLL, 1970b) (Fig. 24A, B) The intercentra are represented by unpaired, crescent-shaped elements, similar to those of *Lohsania* (THOMSON & VAUGHN, 1968) and *Eusthenopteron* (ANDREWS & WESTOLL, 1970a). The notochordal canal is rather wide, and the centra are correspondingly thin-walled (Fig. 24C). Their ventral side is slightly rugose and featureless. The lateral side bears a well-marked ridge in the middle, which might represent the line of attachment for the myoseptum (my ri), separated from the anterior and posterior edges by slight grooves sometimes pierced by nutrient foramina (Fig. 24D).

The pleurocentrum is a paired, small, deep triangle-shaped element (Fig. 24E). Its dorsomedial edge is composed of an unfinished bone margin, that might reflect the cartilaginous nature of the bridge which connects the two halves and separates the notochord from the neural canal. Two articulation facets for the neural arch (na ar) are present: a larger, anterior one and a smaller posterior one, the former being slightly displaced ventrally. The anterior facet might represent the place for the attachment of the neural arch of the same segment, while the posterior one might serve for the attachment with the anterior end of the next neural arch posteriorly. The

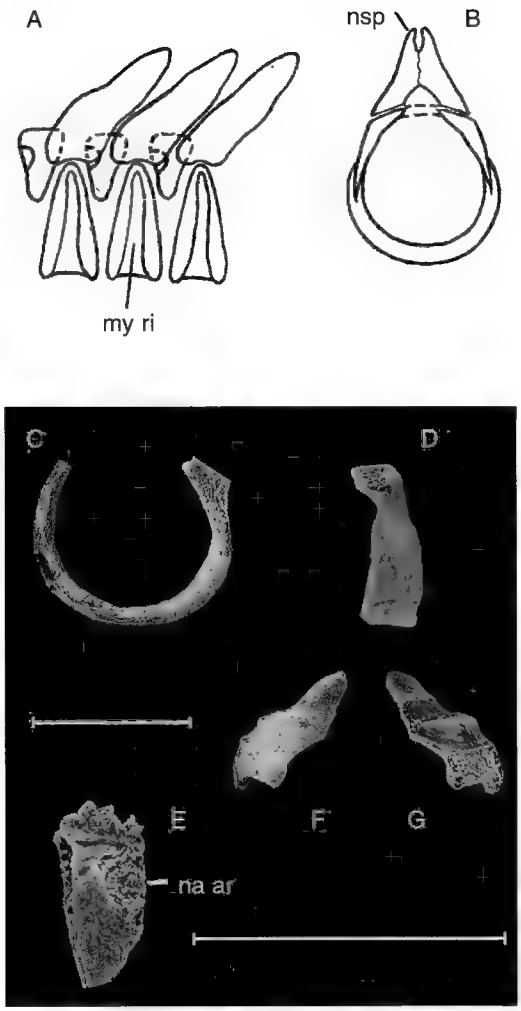

FIG. 24. — *Medoevia lata* n. g., n. sp., elements of the vertebral column. A, B, reconstruction of the vertebrae; C, D, intercentrum; E, pleurocentrum; F, G, neural arch element. A, D, E, F, lateral view; B, C, anterior view; G, medial view. Scale bar: 10 mm.

Medoevia lata *n. g., n. sp., éléments de la colonne vertébrale. A, B, reconstitution des vertèbres; C, D, intercentre; E, pleurocentre. F, G, éléments de l'arc neural. A, D, E, F, vue latérale; B, C, vue antérieure; G, vue médiale. Échelle: 10 mm.*

intersegmental artery or the ventral spinal nerve could pass through a well-marked groove between these two facets.

The neural arches differ from each other by the length and breadth of the neural spines (Fig. 24F). These elements are composed of two separate halves, as in *Osteolepis* (ANDREWS & WESTOLL, 1970b). These were probably connected by means of cartilage, since there is a strip of the bone surface devoid of periosteal lining above the neural canal (Fig. 24G). The median surface of the neural spines is smooth, implying that they were free. The neural arches were probably connected to each other as small, incompletely ossified zygapophysis tubercles are present at the back of the arch, above the neural canal.

SCALES

The scales in *Medoevia* differ significantly from the standard osteolepid pattern (Fig. 25A-H). Their external surface bears a distinct groove separating the overlapped part from the free part. The latter is covered with cosmine, as in typical osteolepids, but the overlapped portion is ornamented with fine ridges, forming an irregular network (Fig. 25A), whereas it is smooth or slightly rugose in the other known osteolepids (e.g. JARVIK, 1948). The internal surface is quite typical for the eusthenopterids and rhizodontids, being ornamented with concentric growth rings, which are best seen in the anterior part of the scale (Fig. 25B). The posterior part of the central area is covered by numerous vascular foramina, and its centre is occupied by a distinct knob. It is often accompanied by a vestige of the weakly developed osteolepid-like articulation ridge which tapers gradually (ar ri + kn), so that there is no articulation process to contact its dorsal neighbour. The posterior margin of the inner surface is smooth. The scales are thin, relatively to their size.

The scales of the anterior dorsal row are rounded or slightly shorter than wide. The overlapped surface may represent up to a half of the total scale length. The flank scales are roughly rhomboid in shape, their corners being rounded (Fig. 25C-F). Some of them are very elongated. The scales which cover the base of the pectoral fin are built in a generally the same manner, but not well enough preserved to add more details. A single small, thick and wedge-shaped scale with a very narrow overlapped portion might represent a basal scute (Fig. 25G– H).

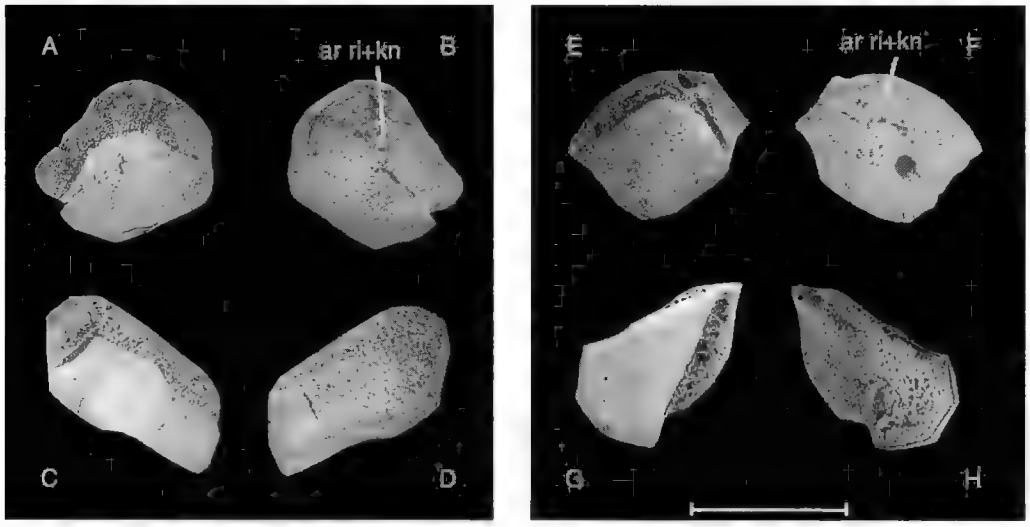

FIG. 25. — *Medoevia lata* n. g., n. sp., scales. A, B, dorsal row scale; C-F, flank scales; G, H, basal scute (?). A, C, E, G, outer surface; B, D, F, H, internal surface. Scale bar: 10 mm.

Medoevia lata *n. g., n. sp., écailles. A, B, écailles de la rangée dorsale ; C-F, écailles des flancs ; G, H, écusson basal (?). A, C, E, G, surface externe ; B, D, F, H, surface interne. Échelle : 10 mm.*

DISCUSSION

The reserach on osteolepiform is historically based on the extremely well studied material on *Eusthenopteron foordi*. For decades the characters of this species were adopted as defining the entire order Osteolepiformes, while the large number of species referred to as the Osteolepididae were practically overlooked because of the poor information of their internal morphology. This resulted in the question whether the Osteolepiformes are paraphyletic or a clade, which was raised several times by various authors, for example JANVIER (1980) and ROSEN *et al.* (1981). The views in the latter paper were opposed by PANCHEN & SMITHSON (1987), who also criticised most of the characters used by ANDREWS (1973) to define the Osteolepiformes, although they accepted two of them (enlarged scutes at the base of the fin lobes and unjointed radials of the median fins) and added a new character: the unique type of cheek plate, composed of seven bones of approximately equal size. Nevertheless, the same condition is observed in the Panderichthyida (VOROBYEVA, 1989; VOROBYEVA & SCHULTZE, 1991) and Rhizodontida (ANDREWS, 1985). LONG (1985a) suggested several characters which he regarded as autapomorphic for the Osteolepiformes, such as a cheek complex including an enlarged lachrymal, the subvertical preopercular, the partially exposed anocleithrum, and the same basal scutes as proposed by ANDREWS (1973). The basal scutes are also known in the Canowindridae (YOUNG *et al.*, 1992), but this group possess more than seven bones in the cheek plate; moreover, the latter character is apparently also present in tetrapods. In *Ichthyostega* (JARVIK, 1952, 1980), *Acanthostega* (CLACK & COATES, 1993) and *Crassigyrinus* (PANCHEN, 1985; PANCHEN & SMITHSON, 1987) there exists a bar-like, subvertical preopercular as well. YOUNG *et al.* (1992) accept the basal scutes and the ornamented dermal anocleithrum of the previous authors and add the presence of a single pair of external nares. The last feature might be used as synapomorphy for osteolepiforms, panderichthyds and tetrapods, but the first two are indeed apomorphic for osteolepiforms. This taxon is thus defined by at least three characters.

1. The presence of the basal scutes at the base of all fins except the caudal one.

2. Unjointed radials of median fins.

3. Large, ornamented anocleithrum.

On the basis of these characters five families are included in the order: Osteolepididae, Eusthenopteridae, Rhizodopsidae, Megalichthyidae and Canowindridae. The Lamprotolepididae may be tentatively assigned here to the Osteolepiformes, yet they are incompletely known.

In order to analyse the osteolepidid-eusthenopterid interrelationships, one has to define which unique features might be used to define the Osteolepididae and in what respect they differ from eusthenopterids (rhizodontids *sensu* JARVIK).

Marsdenichthys longioccipitus Long and *Medoevia lata* n. g., n. sp., display several features which suggest their somewhat intermediate position between these two groups, thereby generating a fairly confusing situation where things seemed to be clear before.

JARVIK (1980) lists several characters, which serve to separate the Osteolepididae from the "Rhizodontidae" (Eusthenopteridae). These include the presence of the extratemporal, the oblique

position of the crista parotica, the connection of the parasymphysial (adsymphysial) dental plate to the vertical lamina of the anterior coronoid, and the presence of rhomboid scales, which all characterize the Osteolepididae. The postspiracular plate, the rostro-caudal direction of the crista parotica, the gap between the adsymphysial plate and the vertical lamina of the anterior coronoid and the cycloid scales characterize the "Rhizodontidae". The similarities between the two groups are numerous and might be recognized either as synapomorphic or symplesiomorphic, depending on the feature under consideration. LONG (1985a) discussed the problem of the relationships between the osteolepidids and eusthenopterids. He stated that one character, the thin cycloid scales devoid of cosmine layer, clearly separates *Marsdenichthys* from all other osteolepidids. Unfortunately, the other characters listed above are not observed in *Marsdenichthys*, because of its incompleteness.

The postspiracular plate is, according to JARVIK (1980), borne by the anterodorsal part of the hyomandibula and belongs to the operculogular series. In *Medoevia* the tabular-extratemporal suture overlays the crista parotica, the latter supporting a large portion of the extratemporal. This leeds us to suggest that this bone either became fused with the tabular in eusthenopterids or disappeared, while the postspiracular is originally independent from it. The direction of the crista parotica is well known only in some osteolepiforms, such as *Osteolepis* (WATSON, 1954), *Megalichthys* (ROMER, 1937; BJERRING, 1972), *Eusthenopteron* (JARVIK, 1954, and later works) *Megapomus* (VOROBYEVA, 1977a), *Jarvikina* (VOROBYEVA, 1960, 1962, 1977a; VOROBYEVA & OBRUCHEV, 1964), *Rhizodopsis* (SÄVE-SÖDERBERGH, 1936), and *Medoevia*. The picture of the *Osteolepis* braincase in WATSON's paper is rather poor and the figured neurocranium gives the impression of being incompletely ossified, so the precise position of this structure is difficult to establish.

Megalichthys and *Rhizodopsis* (although these two genera belong to separate families not reviewed here) show the oblique course of the crista parotica, but in *Eusthenopteron*, *Jarvikina*, *Megapomus* and *Medoevia* the structure under consideration is directed posteriorly. This character is thus variable.

Such features as the contact of the adsymphysial plate with the anterior end of the precoronoid vertical plate seem to be unconvincing, as they vary even intraspecifically, for example in *Chrysolepis orlensis* (LEBEDEV, 1983) and *Chrysolepis* sp. (collection 2921 of the Palaeontological Institute, Moscow; LEBEDEV, pers. obs.), in which both types and the intermediate condition are found. In *Medoevia* this contact is realized.

The complete absence of cosmine over the bone and scale surface is characteristic for the genus *Glyptopomus* (JARVIK, 1950), the same is described by JESSEN (1966) in *Latvius* sp. A. The absence of cosmine cover over the outer surface of the scales is mentioned by JARVIK (1948) in several species of Scottish osteolepidids, such as *Thursius macrolepidotus*, *Osteolepis macrolepidotus* and *Gyroptychius* sp. indet. 2, as a variation. Some of the specimens described, for example *Osteolepis macrolepidotus* (JARVIK, 1948, Fig. 6B, D) display a deviation from the typical osteolepidid scale pattern, being ornamented on the overlapped surfaces and showing no groove that usually separates it from the free surface. The scales of *Gyroptychius* sp. inc. 2 (JARVIK, 1948, Fig. 6C; Pl. 37, Figs. 9, 12) seem to vary from a rhomboid to a cycloid shape, their visceral surfaces being ornamented with the concentric growth ornamentation and a short wedge-shaped boss, which is characteristic for eusthenopterids.

In *Marsdenichthys* (LONG, 1985a, Figs. 2a, b, 6a) the posterior edge of the scales is pointed, as is well seen on the photographs and drawings. The boss on the internal surface is supported by a short ridge (LONG, 1985a, Fig. 6b), as in *Medoevia* (Fig. 25B).

The scales in *Medoevia* apparently display another version of the same evolutionary event, as they retain the primitive continuous cosmine cover, although their general shape is close to that which is regarded typical for eusthenopterids.

The complete loss of cosmine cover in *Glyptopomus*, *Latvius* sp. A and *Marsdenichthys*, its partial resorption in almost all known "standard" osteolepidids, or its reorganization in *Lamprotolepis* and *Viluichthys* (VOROBYEVA, 1977a) show that this process occurred several times in osteolepiform evolution, and that the "cycloidization" and "decosminisation" took place in parallel.

Of the character list proposed by JARVIK (1980) to distinguish between the osteolepidids and eusthenopterids, only the retention of the separate extratemporal seems to be a stable one. This character is, however, observed in the Canowindridae (LONG, 1987; YOUNG *et al.*, 1992).

A character that inequivocally separates eusthenopterids from the osteolepidids, as far as it is known at present, is the mode of junction between the vomers and the anterior part of the parasphenoid. The posterior processes of the vomers are absent, or developed only slightly (for example, in *Gyroptychius pauli*) in osteolepidids, while in all known eusthenopterids these processes extend backwards on either sides of the parasphenoid. The major difference here is in the overlapping pattern. In osteolepidids the anterior part of the parasphenoid is underlain by the posteromedial parts of the vomers. In contrast, in eusthenopterids, the posterior processes of the vomers form the dorsal and ventral shelves, which incorporate the lateral edges of the parasphenoid on both sides, or simply fuse to it by means of a complicated suture (JARVIK, 1937, 1942, 1980; VOROBYEVA, 1977a).

In *Panderichthys rhombolepis* the vomers also possess relatively long posterior processes, but they overlap the parasphenoid dorsally (pers. obs. PIN 2846/2). It may be suggested that this advanced construction evolved to enforce the biting function of the anterior part of the upper jaws in large and active predators.

No apomorphy is thus known to date for the Osteolepididae and the group may be considered paraphyletic with respect to Eusthenopteridae, Rhizodopsidae, Canowindridae, Megalichthyidae and Lamprotolepididae.

In *Medoevia* the hypobranchial 4 articulates with the hypobranchial 3, the posterior face of the basibranchial 2 being entirely occupied by the attachment for hypobranchials 3. This condition is observed in *Glyptolepis groenlandica* (JARVIK, 1963, 1980) and the basibranchial-hypobranchial construction in *Medoevia* displays an intermediate pattern between the latter and that in *Eusthenopteron*, where there are two basibranchials (JARVIK, 1954, 1980). However, this feature is regarded here as either the retention of the condition in the common ancestor to osteolepiforms and porolepiforms, or a parallelism.

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On the neural crest cells of the Australian lungfish

by Anne KEMP

Abstract. — Recent publications referring to the possible importance of the neural crest in the development of dental and skeletal structures in lower vertebrates have placed considerable emphasis on this embryonic tissue. However, a closer examination of the evidence for neural crest involvement in lower vertebrate development suggests that too much emphasis on the part played by the neural crest may be unwarranted. In embryos of at least one of these groups, the dipnoi, the cells of the neural crest may not form a part of the mesenchyme from which the dental and skeletal structures develop.

Keywords. — Neural crest, embryology, dental structures, skeletal structures, dipnoi.

À propos des cellules de la crête neurale chez le dipneuste d'Australie

Résumé. — Les publications récentes qui traitent de l'importance possible de la crête neurale dans le développement de la dentition et du squelette des Vertébrés primitifs ont donné à ce tissu embryonnaire un intérêt considérable. Cependant, un examen plus précis de l'implication de la crête neurale dans le développement des Vertébrés primitifs suggère que trop d'importance est donnée au rôle joué par la crête neurale. Chez les embryons d'un de ces groupes, les dipneustes, les cellules de la crête neurale ne font peut-être pas partie du mésenchyme à partir duquel se développent les structures dentaires ou squelettiques.

Mots-clés. — Crête neurale, embryologie, dentition, squelette, dipneustes.

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INTRODUCTION

In the last few years, there has been increasing interest in an embryonic structure known as the neural crest. This consists of cells which migrate within early embryos from their initial position between cells of the neural plate, that are destined to form the nervous system, and the presumptive epithelium. Evidence for the importance of these cells in development comes mainly from tetrapod embryos, and has indicated a central role for neural crest cells in the formation of organs as diverse as glandular structures, pigment cells, skeletal elements and teeth (LE DOUARIN, 1982). Recent publications on fossil lower vertebrate hard tissue histology have laid considerable emphasis on the importance of the neural crest in forming bone and dental tissue (HALSTEAD, 1987; SMITH, 1991; SMITH & HALL, 1990). However, an examination of the published experimental evidence for neural crest involvement in development of recent vertebrates below the tetrapod level of organisation, and an experimental study of the neural crest in dipnoans, suggest that in fish embryos, the neural crest may not play an important role in the embryological development of organs other than the nervous system (CONEL, 1931, 1942; LAMERS *et al.*, 1981;

SADAGHIANI & VIELKIND, 1990, 1991) or parts of the chondrocranium (LANGILLE & HALL, 1988a, 1988b; NEWTH, 1951, 1956).

Techniques of extirpation of presumptive neural crest cells, cell marking experiments and immunofluoresence microscopy with a mouse monoclonal head neural crest antibody (HNK-1) have been applied to embryos of the recent Australian lungfish, *Neoceratodus forsteri*. This contribution reports preliminary results of these experiments, and indicates the direction of future research. it is also suggested that caution in the use of neural crest theory is advisable when discussing developmental processes and phylogenetic relationships in fossil lower vertebrates.

ABBREVIATIONS

a	archenteron, *archentéron*;
b	blastema of tooth and bone, *blastème dentaire et osseux*;
b	blood cell showing autofluorescence, *cellule sanguine autofluorecente*;
bl	bone blastema, *blastème osseux*;
d	dermal papilla (tooth primordium), *papille dermique (primordium dentaire)*;
e	ectoderm, *ectoderme*;
en	endoderm, *endoderme*;
f	forebrain region, *région cérébrale antérieure*;
h	hindbrain region, *région cérébrale postérieure*;
m	midbrain region, *région cérébrale moyenne*;
me	mesoderm, *mésoderme*;
ms	mesenchyme, *mésenchyme*;
n	notochord, *notochorde*;
nc	neural crest, *crête neurale*;
np	neural plate, *plaque neurale*;
np, nt	nerve tissue, *tissu nerveux*;
nt	nervous tissue, *tissu nerveux*;
o	oral endothelium, *endothélium oral*;
p	peripheral nerve fibre in section, *fibre nerveuse périphérique en section*;
Np	pigment, *pigment*;
t	transverse crest, *crête transverse*.

MATERIALS AND METHODS

Embryos of *N. forsteri* were collected from Enoggera Reservoir, South-East Queensland, (1972-73) and the Brisbane River near Fernvale, also in South-East Queensland, and reared in the laboratory according to the methods described in KEMP (1981). Stages of development follow those described by KEMP (1982). Extirpations and marking experiments were carried out on embryos of stages 17-25, and these were reared subsequent to the operation until stage 48. Stages 17-25 cover development from the earliest appearance of the neural plate, through formation of the neural folds and neural tube and early development of head structures. Stage 48 is a hatchling

with sharp conical teeth and voracious feeding habits, usually feeding on small soft bodied invertebrates. Descriptions of the morphological aspects of neural crest development and immunofluorescence experiments are based on two additional series of fixed embryos from stages 17-46. At the latter stage, tooth development is established, although the hatchling has not yet begun to feed.

Because development of *N. forsteri* is superficially more similar to development of urodele amphibia than to development of other fish embryos, techniques of extirpation and cell marking worked out for urodeles (de BEER, 1946; HORSTADIUS & SELLMAN, 1942; RUGH, 1963; SELLMAN, 1955) were adapted for the present series of experiments on lungfish embryos. Embryos were decapsulated mechanically in sterile Holtfreter's solution and transfered to operating dishes containing a layer of 2% agar covered in sterile Holtfreter's solution. Portions of the presumptive neural crest were removed from the edge of the neural plate or neural folds according to the diagrams in figure 1. At stages 17 and 18 cells were removed from presumptive fore, mid or

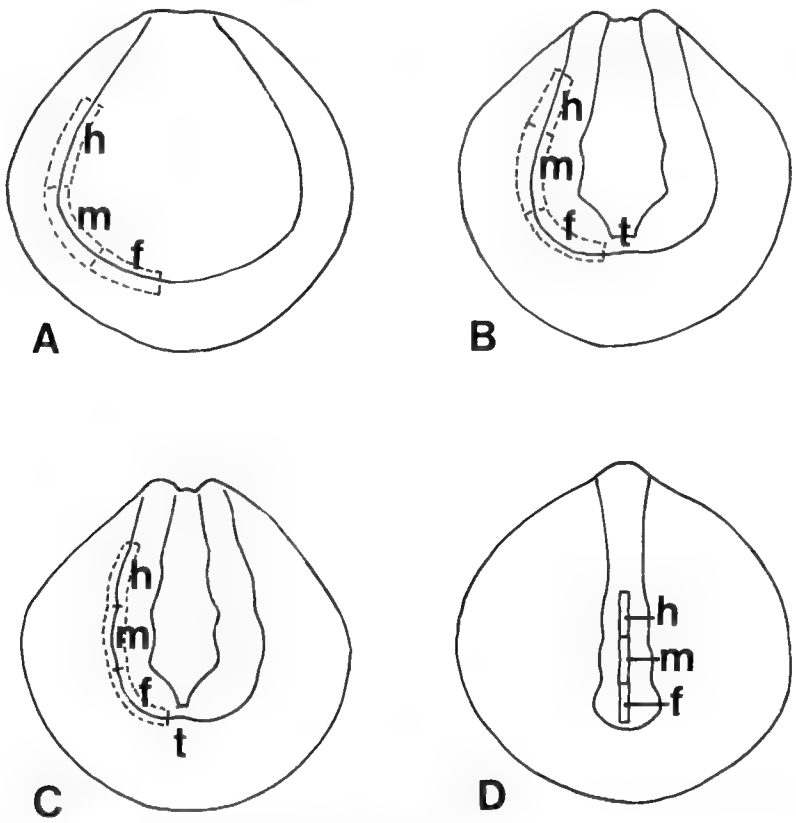


FIG. 1. — Outline drawings of *Neoceratodus forsteri* neurulae showing the areas of neural crest cells extirpated or stained in the experiments. A, stage 17. B, stage 19. C, stage 22. D, stage 25. Scale = 1 mm.

Dessin de la neurula de Neoceratodus forsteri *montrant les aires des crêtes neurales expérimentées A, stade 17; B, stade 19; C, stade 22; D, stade 25. Échelle = 1 mm.*

hind brain regions at the edge of the neural plate (Fig. 1A). From stages 19-23, cells were removed from the crest of the neural folds in presumptive fore, mid and hind brain regions, and from the tranverse crest that lies in the anterior midline of the developing nervous system (Fig. 1B, C). At stage 24 and later, epithelium and underlying tissue above the fore, mid and hind brain regions were extirpated (Fig. 1D). Two series of operations were performed, one involving unilateral removal of cells and the other bilateral. The control series was decapsulated and treated subsequently in the same way, but the embryos were not subjected to extirpation. After the operations, embryos were left in the operating dishes for two hours to permit the edges of the ectoderm and neural folds to seal. They were then transferred to individual crystallising dishes with an agar base and containing sterile Holtfreter's solution, and kept in these dishes until they reached stage 48. Penicillin and streptomycin were added to operating and rearing media at a final concentration of 0.001% of each antibiotic.

For vital staining experiments, dyes were applied to areas at the edge of the neural region of decapsulated embryos (Fig. 1A-C), using methods outlined in RUGH (1963). These experiments were only done on embryos before the neural folds had closed and become covered by epithelium. They were performed in operating dishes and the embryos transferred later to crystallising dishes. Dyes used were Bismarck brown, neutral red, methylene blue and nile blue sulphate.

Embryos used for the descriptive series were fixed in Karnovsky's fixative, washed in buffer, dehydrated in alcohol and embedded in methacrylate resin. Sections were cut at 3 or 4 mm and stained with toluidine blue in phoshate buffered saline at pH 7.4. Embryos used for immunofluorescence experiments were fixed in chilled fixative containing 0.5% glutaraldehyde and 2.5% paraformaldehyde in phosphate buffer (pH 7.4), washed and dehydrated in the cold, embedded in paraffin wax (melting point 56 c) and sectioned at 10 mm. Temperatures were not allowed to rise above 60°C during processing, and specimens were stored at 4°C to maximise protection of the antigens. Immunofluorescence tests with HNK-1 mouse monoclonal egg followed the methods of SADIGHIANI & VIELKIND (1989). Assays were carried out at 4°C to minimise non-specific bonding with antibody. Controls consisted of sections that were treated with non-specific mouse egg instead of HNK-1 mouse egg. A second series of controls using buffer instead of non-specific egg was also used.

RESULTS

NEURAL CREST CELLS IN THE NORMAL LUNGFISH EMBRYO

Uncleaved eggs of *N. forsteri* contain granules of melanin pigment laid down in the developing oocyst and found in the outermost layer of cytoplasm in the fertilised egg. It is most dense in the animal pole of the egg which lies uppermost in the egg membranes. During cleavage it remains mostly in cells of the animal pole (Fig. 2A) and during blastula formation it remains mostly in ectodermal cells. Significant quantities of egg pigment are subsequently found in cells of the presumptive nervous system (Fig. 2B).

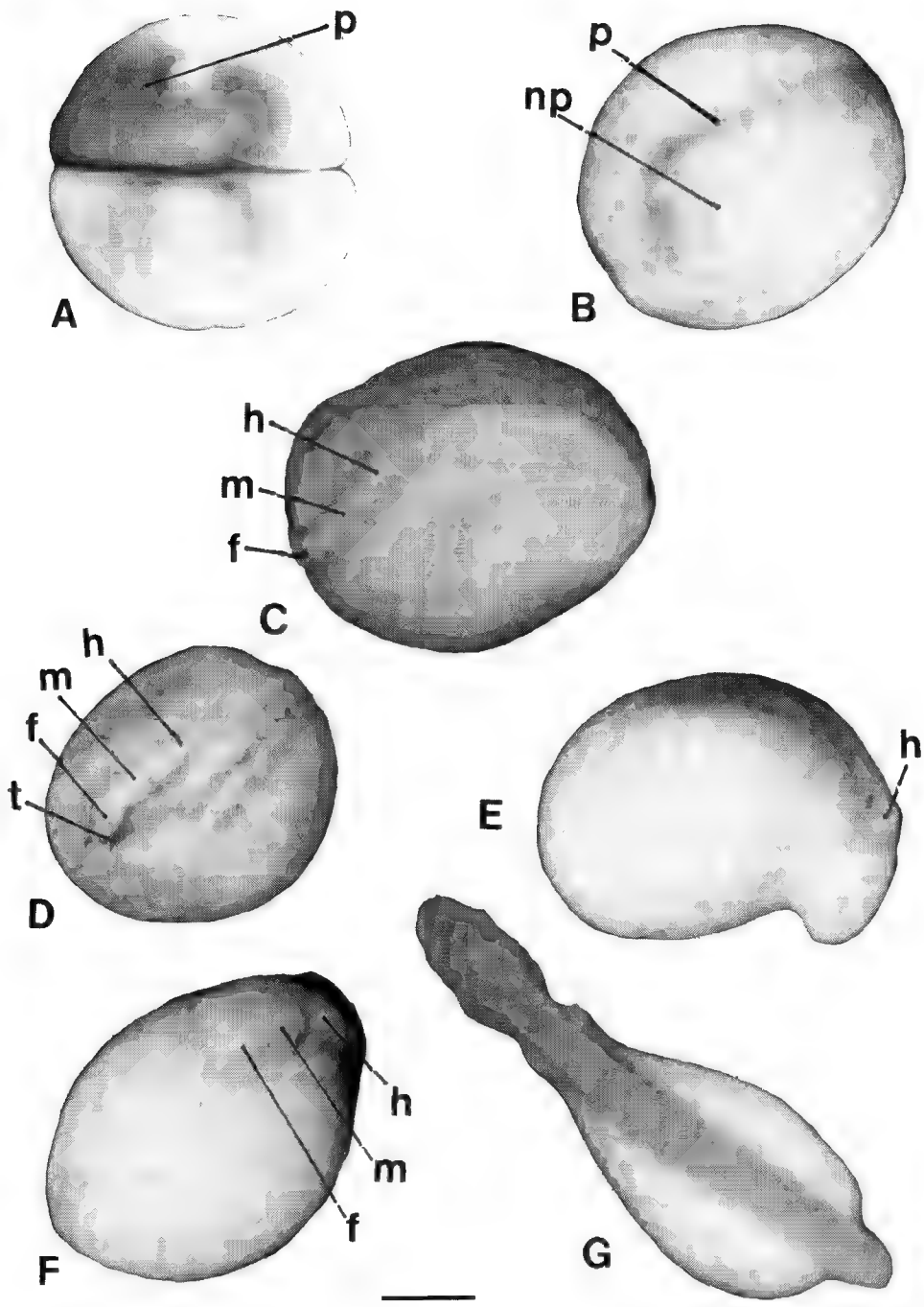
The neural plate in *N. forsteri* is first visible in embryos of stage 17 as a flattened area extending forwards from the slit shaped blastopore, and is quickly delineated by concentration of egg pigment granules lying within the presumptive neural folds (Fig. 2B). As the edges of

the plate begin to form folds the concentration of the pigment granules becomes more obvious. Development of the brain in *N. forsteri* is precocious, and by stage 20 fore, mid and hind brain regions are discernible, although the neural folds are still in an early stage of development (Fig. 2C). As in amphibian embryos (HORSTADIUS & SELLMAN, 1942), a distinct transverse crest develops (Fig. 2D). Closure of the neural folds progresses through stages 21-23 (Fig. 2D) and a neural tube is complete anteriorly by stage 24. Posterior closure follows. At stage 25, the neural tube is covered by epithelium and development of the brain and associated structures is continuing (Fig. 2E, F). by stage 35 (Fig. 2G), the nervous system is already functional at a rudimentary level.

Despite the precocity of brain development, the best that can be said of the neural crest of *N. forsteri* is that there is little of it and that it enters the embryo late. Up to stage 20, there are no migrating neural crest cells (ectomesenchyme cells), nor are there cells of endomesenchyme origin (derived from the endoderm) within the embryo (Fig. 3A, B). Only the primary germ layers of ectoderm, mesoderm and endoderm are present. A section of the presumptive nervous system and associated tissues at stage 17 reveals no neural crest cells (Fig. 3A). A section through the flank of an embryo of stage 20 has only cells of ectoderm, mesoderm and endoderm, and no mesenchyme cells of any type (Fig. 3B).

Neural crest cells begin to move inwards at stage 20, from the forebrain region, but not from the transverse crest, mid or hind brain vesicles or from the presumptive spinal cord. In subsequent stages, the process of invagination of neural crest cells continues, involving the nerve cord of progressively more posterior regions. These cells are clearly ectodermal in origin, with small yolk globules and some pigment granules. They remain close to the neural folds, and are soon organised into cranial and spinal ganglia. At stage 20, and later, additional free cells are present within the embryo, between the ectoderm and the mesoderm of the head region, but these are associated with developing foregut or mesoderm, and contain large quantities of sizeable yolk globules, too large and too many for the cells to have been derived from ectoderm. Further research on this subject is continuing, but it could be that the bulk of the mesenchyme is derived from mesoderm or endoderm in this lungfish.

Ectomesenchyme and endomesenchyme cells can be distinguished at early stages of development by the differing number of granules of egg pigment and the different sizes and numbers of yolk globules that they contain. Ectomesenchyme cells have larger numbers of pigment granules, and endomesenchyme cells have larger and more yolk globules. Each mesenchyme resembles the cells from which it originates. Ectomesenchyme and endomesenchyme start to appear within the embryo at stage 23, when the neural folds begin to close, as a few scattered cells in the spaces between the ectoderm and the developing internal tissues. Ectomesenchyme cells are not numerous, and resemble the cells of the neural tissue, from which they apparently originate (Fig. 3C), in numbers of granules of egg pigment and in the sizes and numbers of yolk globules. By stage 36, cells with relatively numerous and large yolk globules are common within the embryo, and it is difficult to distinguish any with the characteristics expected of ectomesenchyme cells (Fig. 3D). Following the fate of mesenchyme cells by methods of light microscopy alone in dipnoan embryos is unfortunately no longer possible after the neural folds have closed and tissues and organs have begun to differentiate within the embryo. As development continues, the yolk and egg pigment profiles so characteristic of early development become less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reliable as indicators of tissue of origin (ectomesenchyme or endomesenchyme). Yolk globules are quickly used up, particularly in the most actively developing cells, as a source of nutrients for growth and differentiation. Granules of egg pigment are passed from cell to cell and are eventually voided by epithelial cells or into the gut lumen. Endomesenchyme and ectomesenchyme cells soon look alike, and are lightly yolked with a scattering of egg pigment granules within the cytoplasm. By stage 40 (Fig. 3E), before organogenesis has produced recognisable dental and skeletal tissues in *N. forsteri*, the origin of the mesenchyme cells that will play a part in the development of those tissues cannot be determined on characteristics visible in the light microscope. Few of the mesenchyme cells have any yolk left, though most of the cells of the oral endothelium are still heavily yolked (Fig. 3E). By the time tooth and jaw primordia can be distinguished, at stage 44, the oral endoderm has almost lost its distinctive features as well (Fig. 3F).

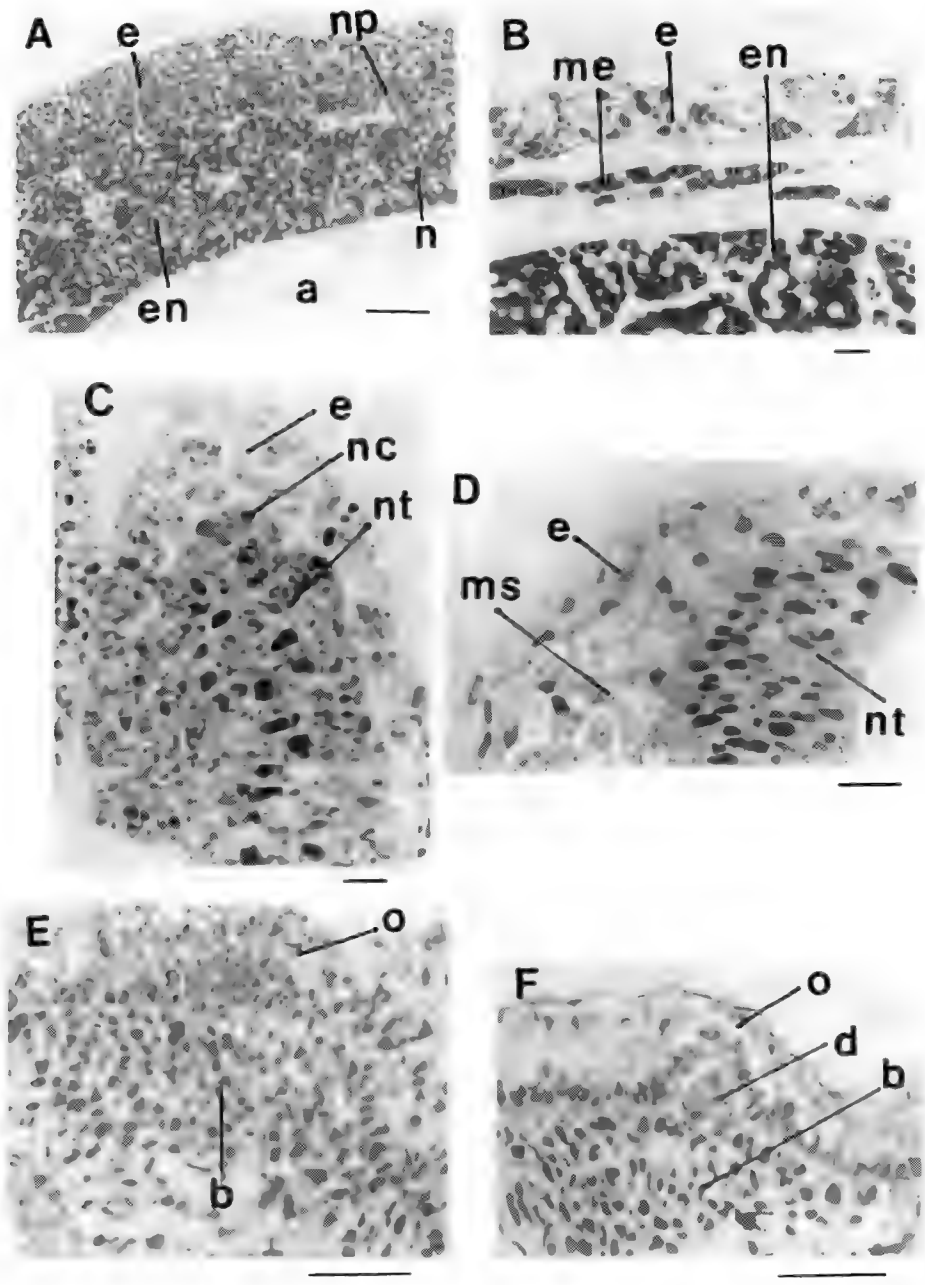
EXTIRPATION EXPERIMENTS

Extirpations of presumptive neural crest were performed in embryos of stages 17-25, ranging from embryos in which the neural folds were barely discernible, to stages in which migration of crest cells and development of brain and associated structures is advanced. Since development of the primary brain vesicles in *N. forsteri* is so precocious, division of the presumtive brain region into fore, mid and hind brain areas is possible well before the neural crest cells start to migrate. Early experiments involving the removal of large amounts of tissue resulted in the death of the operated embryos within a few days, and extensive extirpation of material was discontinued. Later experiments involved the removal of only small amounts, and ablations were restricted to the removal of groups of cells at the edge of the plate or folds, or at the crest of the neural tube. Damage to presumptive neural tissue within the folds was avoided, as early experiments showed that *N. forsteri* embryos are unable to tolerate such injury.

Experiments were carried out as eggs became available, beginning in 1972 and 1973, and continuing in 1978 and in subsequent years. Season by season, the results were the same. Ablation of presumptive neural crest tissue, performed at any stage between 17 and 25, had the same effect. The experiments were all negative. Operated fish (Fig. 4A) grew and developed as well as controls (Fig. 4B). They had normal pigment patterns, normal sense organs, and normal head morphology. The chondrocrania of hatchlings that develop from operated embryos have the same structure as those that develop in control embryos The extirpations performed on lungfish embryos in these experiments had no measurable effects on subsequent development.

FIG. 2. — Photographs of normal embryos of *N. forsteri*. A, stage 2-3, showing egg pigment at the surface of the animal pole region where cleavage furrows are forming. B, stage 18 showing egg pigment concentrated within the developing neural plate. C, stage 20 showing fore, mid and hind brain regions of the developing neural folds. D, stage 23 showing transverse crest, fore, mid and hind brain vesicles of the closing neural folds. E, stage 25 in lateral view showing prominent hind brain region. F, stage 25 in ventral view showing fore, mid and hind brain. G, stage 35 in dorsal view. Scale = 1 mm.

Photographies d'un embryon normal de N. forsteri *A, stade 2-3 montrant le pigment de l'œuf en surface et la région du pôle animal où s'amorce la segmentation. B, stade 18 montrant la concentration du pigment de l'œuf et le développement de la plaque neurale. C, stade 20 montrant les régions antérieure, moyenne et postérieure du cerveau et le développement des replis neuraux. D, stade 23 montrant la crête transverse, les vésicules cérébrales antérieure, moyenne et postérieure du tube nerveux se refermant. E, stade 25 en vue latérale montrant la région postérieure du cerveau. F, stade 25 en vue ventrale montrant les régions antérieure, moyenne et postérieure du cerveau. G, stade 35 en vue dorsale. Échelle = 1 mm.*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Cells marking experiments

Vital dyes used traditionally to stain living cells of amphibian embryos did not work with embryonnic cells of *N. forsteri*. Bismarck brown was too close to the natural background colour of the embryo to be useful as a cell marker. Neutral red did not stain the cells. Methylene blue and nile blue sulphate had the effect of a refined extirpation, because the stained cells died and were sloughed off by the embryo. Attempts to mark neural crest cells in lungfish embryos with these dyes were abandoned early in the project, as suitable eggs were scarce.

Immunohistochemistry

Immunofluorescence studies of fixed, normal lungfish embryos gave a partial answer to the question of neural crest involvement in development of these fish. HNK-1 antibody produces a positive response in certain cells and tissues of *N. forsteri* embryos. In early stages, while the neural tube is closing and the brain is differentiating, cells that are destined to form parts of the nervous system and some of the mesenchyme cells react positively to HNK-1, although the reaction is weak. The quantity of yolk globules and the small amounts of cytoplasm present in all of the cells in early stages of development make detection of a positive result difficult, and neural crest cells are not present in large numbers. Even at this early stage, most of the mesenchyme cells are negative. In later stages, when organogenesis is beginning, the response to HNK-1 antibody is more localised. At stage 44, when the skeletal tissues are beginning to form, and dermal papillae are present under the oral endothelium, only those structures that are part of the nervous system, the brain, spinal cord, cranial ganglia or peripheral nerves, as well as sense organs like the eye, fluoresce when tested with this antibody (Fig. 4C). Other tissues of the head, with the exception of red blood cells within blood vessels, do not show fluorescence. Dermal papillae, mesenchyme cells below the papillae, and oral endothelium is uniformly negative. The same result is obtained at stage 46, when extracellular matrix of tooth, bone and cartilage has begun to appear (Fig. 4D). Cells associated with the nervous system are positive, and cells associated with the developing skeletal structures are negative. Branches of the peripheral nervous

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Fig. 3. — Photomicrographs of sections of normal *N. forsteri* embryos showing distribution of ectomesenchyme and endomesenchyme. A, detail from the head neural plate region in an embryo of stage 17: no neural crest cells are present. B, detail of section through the flank of an embryo of stage 20 showing ectoderm, mesoderm and endoderm cells. C, detail of the closing neural folds in the head region of an embryo of stage 23 showing neural crest cells migrating from the developing nervous system. D, section through the developing hind brain of an embryo of stage 36 showing increase in amount of mesenchyme and loss of distinctive characters of the cells. E, blastema below the foregut endoderm of an embryo of stage 40, in the region of the developing tooth primordia, mesenchyme cells have no yolk left, but the oral endothelium is heavily yolked. F, tooth and jaw blastema at stage 44, showing a single dermal papilla (tooth primordium), oral endothelial cells still contain yolk. Scales = 0.1 mm.

Photographies au microscope optique de coupes d'embryon normal de N. forsteri montrant la répartition de l'ectomésenchyme et de l'endomésenchyme. A, détail de la région antérieure de la plaque neurale d'un embryon au stade 17 : absence de cellule de la crête neurale. B, détail d'une coupe au travers du flanc d'un embryon au stade 20 montrant les cellules de l'ectoderme, du mésoderme et de l'endoderme. C, détail de la fermeture des feuillets neuraux de la région de la tête d'un embryon au stade 23 montrant la migration des cellules de la crête neurale à partir du système nerveux embryonnaire. D, coupe à travers la région postérieure du cerveau d'un embryon au stade 36 montrant une concentration de mésenchyme et une perte de l'individualisation des cellules. E, blastème situé ventralement au tube digestif antérieur endodermique d'un embryon au stade 40, dans la région du développement du primordium dentaire, les cellules mésenchymateuses ne présentent aucun reste de vitellus mais l'endothélium de la région orale est chargé de vitellus. F, blastème dentaire et de la mâchoire au stade 44 montrant une papille dermique isolée (primordium dentaire) ; les cellules endothéliales orales contiennent encore du vitellus. Échelle = 0,1 mm.

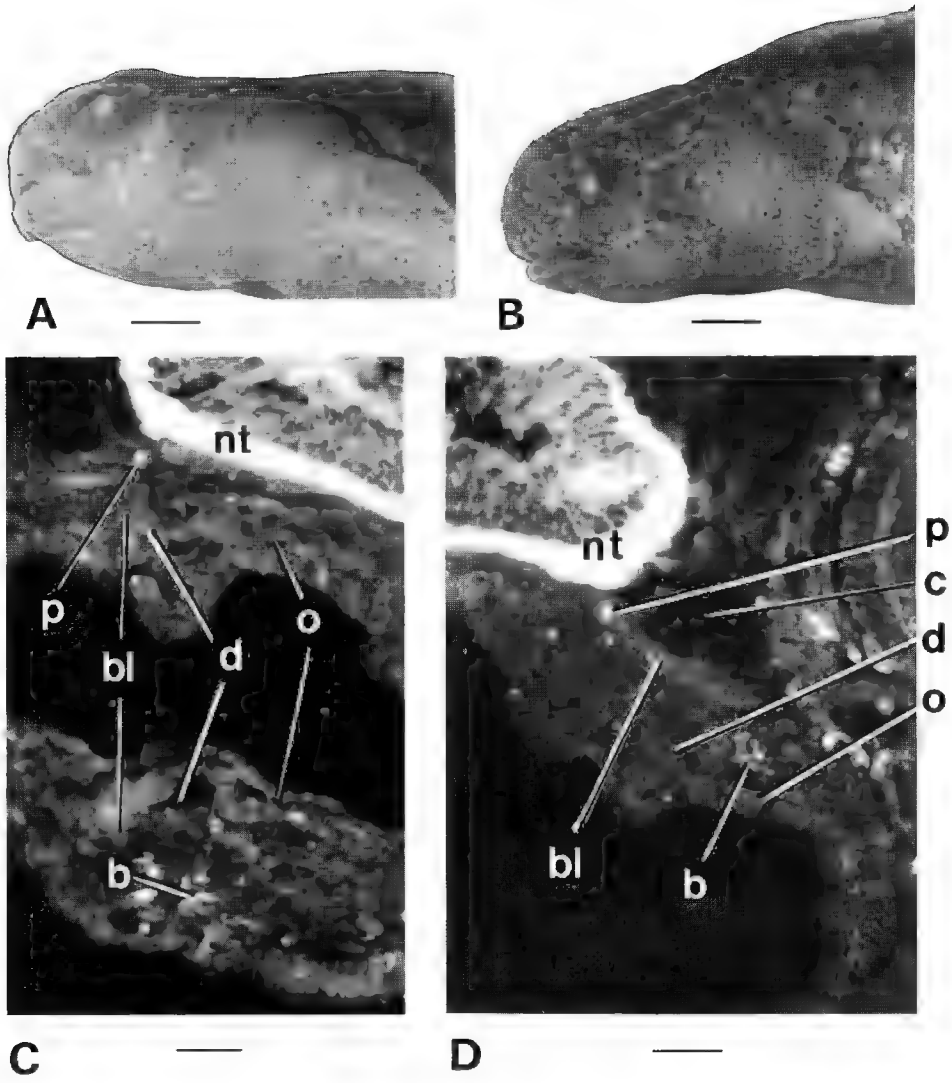

FIG. 4. — Experimental and control hatchlings of *N. forsteri*. A, an apparently normal hatchling developing from an embryo in which the midbrain crest was removed at stage 19. B, a normal hatchling of stage 48 developing from a control embryo decapsulated at stage 19. C, a section through the mouth region of a hatchling of stage 44, reacted with HNK-1; neural tissue shows fluorescence, and mesenchyme cells of tooth and bone blastema do not. Circular spots on the photograph are contaminants. D, section through the head region of a hatchling of stage 46, reacted with HNK-1, neural tissue shows fluorescence, and developing tooth cusps, bone blastema and cartilage cells are negative. Circular spots are contaminants. Scales = 0.1 mm.

Contrôle et expérimentation de nouveau-nés de N. forsteri. *A, nouveau-né apparemment normal provenant d'un embryon qui a subi l'ablation de la crête du cerveau moyen au stade 19. B, un nouveau-né normal de stade 48 développé à partir d'un embryon décapsulé au stade 19. C, coupe à travers la région de la bouche d'un nouveau-né au stade 44, réactivée avec HNK-1 : le tissu neural présente une fluorescence à l'inverse des cellules mésenchymateuses des blastèmes dentaires et osseux. Les tâches circulaires sont des contaminations. D, coupe de la tête d'un nouveau-né de stade 46, réactivée avec HNK-1 : le tissu neural montre une fluorescence et le développement des dents, les blastèmes osseux et les cellules cartilagineuses sont en relief. Les tâches circulaires sont des contaminations. Échelle = 0,1 mm.*

sytem within a blastema are positive, but the blastema cells themselves are not (Fig. 4C, D). Melanin cells below the skin and mesenchyme cells in other parts of the body are also negative. With the exception of red blood cells, which exhibit autofluorescence in control and experimental sections, cells and tissues in control sections are uniformly negative.

DISCUSSION

Evidence for the existence of neural crest cells in fish embryos is based historically on light microscopy, and there is little doubt that neural crest cells migrate in embryos of lower vertebrates as they do in higher vertebrates (KASTCHENKO, 1888; LOPASHOV, 1944). Considered opinion on the early studies of the neural crest supported a limited role in development for the neural crest in lower vertebrates, and GOODRICH (1930) recommended caution in the interpretation of the results of studies into the neural crest. Additional evidence of the importance of the neural crest in development of fish and agnathans is based largely on extirpation experiments (NEWTH, 1951, 1956; LANGILLE & HALL, 1988a, b). However, an apparently positive result in such experiments is no more reliable than an apparently negative one. If the part extirpated is small, regulation may occur. Other cells are able to take the place of the ablated material, and the embryo may develop normally despite the deficiency. If the part extirpated is large, the operation may interfere with the normal development of the animal, and give incorrect results because the embryo has developed pathologically. Since the presumptive neural crest is so close to the neural plate, removal at the same time of significant amounts of tissue destined to form parts of the brain is hard to avoid, and this increases the possibility of abnormal development.

Removal of tissue presumed to be responsible for the development of certain structures in an embryo has always been the classical method of determining the origin of a tissue. It is concluded that the extirpated material was responsible for the structure if this structure is missing after the operated embryo has been allowed to develop for a reasonable length of time. This method is, in practice, as crude as it sounds, because of the possibility that the embryo is unable to continue normal development for reasons that have nothing to do with the missing cells. As a result, extirpation of presumptive cells has fallen out of favour with experimental embryologists, especially now that more sophisticated methods of analysis of developmental processes are available (ERICKSON, 1986).

The negative results obtained in the extirpation experiments with *N. forsteri* embryos have several possible explanations. It is possible that the quantity of presumptive neural crest cells removed was so small that the cells left behind were able to take over the function and fate of the missing cells. In other words, dipnoan embryos are capable of regulation. A second possibility is that the neural crest is not particularly important in lungfish for the development of tissues and organs outside the nervous system. The extirpation experiments do not answer the fundamental question of which organs in dipnoan embryos receive a contribution of neural crest cells in the normal course of events. Nor can this be determined by observation of cell characteristics, because these change as development proceeds. The question of the origin of head structures like the cranial ganglia, peripheral nerves and the mesenchymal blastema of skeletal and dental tissues has to be tackled indirectly.

Marking of presumptive neural crest cells in some way prior to migration and following the marked cells in the developing embryo has been used frequently in embryos of higher vertebrates. However, this technique is open to serious error, not the least being the transfer of marker from one cell to another during development (WESTON, 1967). Other constraints include the use of markers that do not harm the cells or alter normal behaviour of the marked cells during morphogenesis. The agent used should be easily visualised in whole or dissected embryos, and should be preserved in situ for histological examination (WESTON, 1967). Most fish embryos are notoriously difficult to manipulate in this way, and lungfish embryos are no exception. However, sophisticated marking techniques using new stains are now available. Minute amounts of these stains are injected into the cells of living embryos, and these are then allowed to continue normal development. The stain can later be visualised after the cells have moved around in the embryo. This technique involves minimal interference with embryological processes, and is currently being tested on lungfish embryos.

New advances in immunofluorescence microscopy have allowed the use of an elegant and simple technique to follow movements of the neural crest cells in developing fish embryos without interfering with the normal course of development. HNK-1, a mouse monoclonal antibody, binds with receptors on and within cells of fish and amphibian embryos and can be visualised by attaching a fluorescein labelled antibody to the primary antigen-antibody complex. After the reaction, cells that carry the relevent antigen show fluorescence in ultraviolet light, and cells that have no antigen do not. This technique, applied to cells of *Xiphophorus* embryos by SADAGHIANI & VIELKIND (1989), relies on the presence of an antigen in the neural crest cells of fish embryos that will react with an antibody, HNK-1, developed against the neural crest cells of higher vertebrates. These authors used the antibody successfully to trace the initial migration of neural crest cells in teleost embryos. They did not follow the cells to the target organs. In a later paper, these authors used immunofluoresence labelling in whole mounts of three species of teleost fish, *Xiphophorus maculatus*, *Xiphophorus helleri* and *Cryzias latipes*, to follow streams of neural crest cells in developing embryos (SADAGHIANI & VIELKIND, 1990a). Cells following a lateroventral pathway entered the pharyngeal gills and the intestinal wall. Neural crest cells in the trunk accumulate around somites and then migrate ventrally, and some of these cells may be pre-melanocytes and precursors of the lateral line. Most neural crest cells were traced to tissues associated with the nervous system. They also state that a small number of cells from the rostral streams may represent cells that participate in the formation of the cephalic skeleton. Growth of explanted neural crest cells in vitro (SADAGHIANI & VIELKIND, 1990b) provides no additional information on the fate of teleost neural crest cells. A study of another teleost, the cyprinid *Barbus chonchonius*, using cell marking and transplantation techniques (LAMERS *et al.*, 1981), indicates that neural crest cells in this species are involved in the formation of a number of tissues, mostly associated with the nervous system and the adrenal gland, but not bone, teeth or cartilage.

The present preliminary result using immunofluorescence techniques in *N. forsteri* suggests that neural crest cells of this species are not responsible for the formation of dental and skeletal tissues. Their role in *N. forsteri* seems to be confined to the formation of cranial ganglia and peripheral nerves. This result is not particularly surprising in view of the evidence from a study of sections of developing embryos, and of the negative results of extirpation experiments. The

normality of the operated embryos shows incidentally that lungfish are capable of regulation. Further experiments on *N. forsteri* embryos, using more specific antibodies to cell adhesion molecules are currently underway.

It is possible that mesenchyme cells in *N. forsteri*, destined to form dental and skeletal structures, do actually originate from the neural crest, and react positively to HNK-1 antibody in an early stage of development, during the migration phase when they cannot be recognised as presumptive dental and skeletal structures, and later lose their reactivity. However, cells that form the cranial ganglia and peripheral nerves retain the ability to react positively even after the ganglia and nerves have begun to differentiate. SADAGHIANI & VIELKIND (1990a) note that the neural crest epitope can be lost from non-neural derivatives of the neural crest as migration proceeds, and that HNK-1 antibody can also recognise cells that are not of neural crest origin. Clearly more extensive and precise studies are necessary.

It may be that lungfish are so unchanged in an evolutionary sense, and so far from the main stream of vertebrate evolution that their neural crest cells are atypical. However, if lungfish are not phylogenetically aberrant, these results could have significant implications for embryological theory in that they suggest that there may be an evolutionary progression in the importance of the neural crest in vertebrate development. It may be that, in lower vertebrates the function of the neural crest is limited to the formation of the cranial ganglia and peripheral nerves, as GOODRICH (1930) recognised. Alternatively, neural crest cells may play a role only in the induction of tissue in the lower vertebrate embryo. However, the actual involvement of neural crest cells in the genesis of diverse organs in primitive fishes has yet to be proved beyond doubt, and elaborate hypotheses based on the importance of the neural crest in formation of the complex dental and skeletal structures of fishes may well be premature.

New studies on the hard tissue microstructure of fossilised lower vertebrates (SMITH, 1991) and of conodonts (SANSOM, 1991; SANSOM *et al.*, 1991) have assigned a central role to the function of cells derived from the neural crest in the formation of dental and skeletal structures in these species. These researchers no longer refer to the role of the neural crest in the formation of the skeletal elements of conodonts in their most recent contribution, (SANSOM *et al.*, 1992), but the earlier statements are made despite the dearth of closely related living relatives of these fossils in which the assertions could be tested experimentally. Even in living species of lower vertebrates, the evidence for the involvement of neural crest cells in bone and in dental structures is not particularly conclusive. NEWTH (1951, 1956), working with lampreys that have no bone and no teeth, and LANGILLE & HALL (1988) working with a teleost, *Cryzias latipes*, that has both bone and teeth, describe the contribution of neural crest to the chondrocranium only, and their work is based on extirpation experiments. The latest reviews on this subject do not provide additional evidence on the contribution of neural crest cells to bones and teeth of fish (ERICKSON, 1986; HALSTEAD, 1987; SMITH & HALL, 1990). The first paper is a general review that does not emphasise lower vertebrates, and the last two simply reiterate the statement that dental and skeletal structures in fishes are derived from cells of the neural crest. There is now some evidence to suggest that neural crest cells may not be important for the formation of dental and skeletal structures of at least one species of primitive vertebrate, the Australian lungfish, *N. forsteri*. It may be that, in primitive vertebrates, the neural crest theory has as little relevance as the now outdated germ layer theory. Fortunately, analysis of cell interactions and the controlling mech-

anisms operating during differentiation and morphogenesis provide more stimulating and important questions for future research (BARD, 1990).

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Acanthostega gunnari, a primitive, aquatic tetrapod?

by Jennifer A. CLACK and Michael I. COATES

Abstract. — The status of the Upper Devonian *Acanthostega gunnari* as a tetrapod is considered in the light of the apomorphic characters which it shares with other tetrapods, and of the plesiomorphic characters which it retains in common with osteolepiform fishes. It shares about two-thirds of the characters recently listed as tetrapod autapomorphies. Of the plesiomorphic features which it retains, some may be truly primitive, whereas others may be associated with secondary modification for an aquatic habitus. After consideration of these characters, we conclude that parsimony demands that they be interpreted as primitive. We then address the question of how tetrapods may be defined, given the likely discovery of more transitional forms in the future. Possession of digits remains the most compelling character in practice at the present, but we point out its potential inadequacies for the future.

Keywords. — Greenland, Upper Devonian, tetrapod, systematics, parsimony, aquatic habitus.

***Acanthostega gunnari* est-il un tétrapode aquatique primitif?**

Résumé. — Le statut de tétrapode d'*Acanthostega gunnari* du Dévonien supérieur est analysé à la lumière des caractères apomorphes qu'il partage avec les autres tétrapodes, et des caractères plésiomorphes qu'il partage avec les ostéolépiformes. Il possède environ les deux tiers des caractères dérivés définis chez les tétrapodes. Parmi les caractères primitifs qu'il présente, certains le sont réellement, mais d'autres pourraient être interprétés comme des adaptations à la vie aquatique. Une analyse parcimonieuse de ces caractères impose de les considérer comme des caractères primitifs. Nous posons alors la question de la définition des tétrapodes, si l'on considère comme probable la découverte d'autres formes intermédiaires dans le futur. La présence de doigts reste le caractère le plus contraignant, tout en soulignant son insuffisance pour le futur.

Mots-clés. — Groenland, Dévonien supérieur, tétrapode, systématique, parcimonie, vie aquatique.

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INTRODUCTION

The origin of tetrapods is one of the perennial problems of vertebrate palaeontology and it has been addressed from many points of view. When did tetrapods arise? How did their many apparently unique features evolve from those of a fish ancestor? Why did tetrapods invade the land? (For a review of some of these, see COATES & CLACK this volume.) From which group of fishes did they evolve, and who are their closest living relatives? (For example, WATSON, 1926; WESTOLL, 1943; ROSEN *et al.*, 1981; SCHULTZE, 1987; PANCHEN & SMITHSON, 1987; FOREY *et al.*, 1991 and references therein). Many of these problems have been plagued by a dearth of data until very recently. *Ichthyostega* from the Upper Devonian of East Greenland, described first by SÄVE-SODERBERGH (1932) and subsequently by JARVIK (1952, 1955, 1980),

has provided most information, with tantalising scraps from other parts of the world (CAMPBELL & BELL, 1977; LEBEDEV, 1984, 1985; AHLBERG, 1991; AHLBERG *et al.* 1994). This was all that represented this most crucial event of vertebrate evolution.

One problem which had not been considered, partly as a result of this lack of data, was precisely how tetrapods are defined. Tetrapods, considered monophyletic by the majority of workers (e.g. WESTOLL, 1943; THOMSON, 1968; GAFFNEY, 1979, ROSEN *et al.*, 1981; PANCHEN & SMITHSON, 1987; SCHULTZE, 1991, but see JARVIK, 1980 for a contrary opinion), have been characterized by a large number of unique characters which distinguish them from their nearest fish relatives (whichever group that is considered to be). The question of how one might categorize an animal which possessed only some of these characters had not been addressed. To put it another way, at what point during the evolution of the group can an animal strictly be called a tetrapod? Is there a single character which constitutes the *sine qua non* for tetrapods, and how should it be recognised? With the lack of data on early tetrapods, this had never arisen as a potential problem among fossil animals. A further related question, likewise hampered by the paucity of the fossil record, involves the sequence in which the unique characters of tetrapods arose, how characters might be interdependent, which were acquired in relation to terrestrialisation and which preceded it.

Acanthostega gunnari is a second genus from the Upper Devonian of East Greenland (JARVIK, 1952). Remarkable material has been recovered from the Britta Dal formation, Gauss Halvø (BENDIX-ALMGREEN *et al.*, 1990), and includes information on most of the skeletal anatomy of this form. *Acanthostega* has proved to be satisfyingly primitive (CLACK, 1989), illuminatingly unconventional (COATES & CLACK, 1990) and unprecedentedly fish-like (COATES & CLACK, 1991) for a tetrapod. It provides a new perspective on the acquisition of tetrapod characters, both in terms of the sequence and the circumstances in which they arose and requires us to look again at the definition of the group, since in many respects it appears to be a transitional form. Below we consider first, how *Acanthostega* measures up to previous diagnoses of tetrapods, then we consider whether it is primitively or secondarily aquatic in those features in which it is fish-like, and thirdly we give some thought to which, if any, single character could be considered to define tetrapods as a group.

Acanthostega AND THE APOMORPHIES OF TETRAPODS

Three papers, published over the last several years have given analyses of the apomorphies of tetrapods. All of them accept the monophyly of tetrapods, as it is accepted here. The first of them was by GAFFNEY (1979), who attempted to test the monophyly first of tetrapods as a whole, then a subgroup within this which he called Neotetrapoda. He gave a list of 11 characters for the first set and five for the second. The second paper was that of PANCHEN & SMITHSON (1987) whose analysis formed part of a wider assessment of the relationships of tetrapods to fish groups. They accepted many (though not all) of GAFFNEY's characters and added three others. GODFREY's account (1989) of the postcranial skeleton of *Greererpeton* listed a total of 41, which included most of those cited by GAFFNEY and PANCHEN & SMITHSON, along with a substantial

number of new ones. His character list was included in an appendix without discussion or references, though many of the postcranial characters were mentioned in the text. SCHULTZE (1987, 1991) commented further on GAFFNEY's and PANCHEN & SMITHSON's papers in an attempt to characterize a plesiomorphic tetrapod.

In addition to the apomorphies listed by the above authors, CLACK (1988) suggested two other characters of the lower jaw which appeared to be unique to tetrapods. These characters are listed with references in table 1. One point to note is that a single character of one author might be split into several by another, making straightforward counting of characters impossible. This, of course, has implications for any parsimony analysis, and emphasises how difficult it is to choose the most parsimonious cladogram from among a number of competing attempts.

Much of the skeleton of *Acanthostega* is now understood, and can be compared directly with these lists For brevity, GODFREY's list is used as the basis of comparison; individual characters are discussed as necessary, in the order and with the numbers in which GODFREY listed them.

It can be seen that *Acanthostega* possesses the majority of the apomorphies listed by GODFREY, but lacks a significant number of others. Those which *Acanthostega* shares unequivocally with other tetrapods will not be discussed further.

7. "No operculum".

It is not clear exactly what GODFREY meant by this character, but we take it to refer to the loss of the operculogular series which covers the gill chamber in fishes, rather than the small bone which articulates with the fenestra ovalis and stapes in Lissamphibia. As the former, it requires some discussion in the light of discoveries about the branchial series of *Acanthostega*. COATES & CLACK (1991) suggested the possibility that *Acanthostega* retained a functional gill-apparatus and an open opercular chamber, based on evidence from the branchial skeleton and shoulder girdle. This implies retention of an opercular flap, though of soft tissue as in larval or paedomorphic urodeles and the more derived modern lungfishes. This cannot be fully tested by fossil material, however. JARVIK (1980) described a subopercular in *Ichthyostega* so that complete loss of the bony opercular series cannot be an apomorphy of tetrapods, but only of a subgroup as GAFFNEY (1979) suggested.

JARVIK (1952) described *Acanthostega* as retaining a preopercular bone in the suspensorium. We assume the homology of this bone to the fish preopercular to be correct, and can confirm its presence in our material. It is also present in the holotype of *Crassigyrinus* (PANCHEN, 1973, 1985) and in *Ichthyostega* (JARVIK, 1980). Though the bone is not part of the opercular series, retention is a primitive character and it is lost in other tetrapods.

11. "A fenestra ovalis in the otic capsule (?), not yet known in *Ichthyostega* or *Crassigyrinus*".

Despite relatively well-preserved material, the relevant region in *Acanthostega* is also poorly known (CLACK, 1992), but as LOMBARD & BOLT (1992) point out, it is poorly preserved in most early fossil tetrapods, and its presence has been reconstructed in most of those in which it has been described. One exception to this is *Greererpeton burkemorani* (SMITHSON, 1982). The origins, homologies and history of the fenestra ovalis deserve further study, but until then should not be taken unquestioningly as a tetrapod apomorphy.

13. "Unossified laterosphenoid region of the braincase".

GODFREY cites CLACK & HOLMES (1988) for an alternative view. They suggested that the degree of ossification of the braincase was not very reliable as a taxonomic character among different groups of tetrapods. *Acanthostega* appears to possess an ossified laterosphenoid region, but the significance of this is uncertain. This character is unreliable as a tetrapod apomorphy.

16. "Some lateral line organs (neuromast system) held in canals, no longer covered by bone (lower mandible)".

In *Acanthostega*, all the lateral lines on the skull and lower jaw, with the exception of a short section on the jugal/postorbital, were held in tubes running through the bone, as they were in *Ichthyostega*. These two earliest tetrapods therefore retain what is usually regarded as the fish-like condition. In *Greererpeton*, some of the canals were still held in tubes, though most were exposed in grooves. This character-state seems to be variable among early tetrapods. Neuromasts lying in open grooves are known among modern fishes, and although their distribution is not entirely consistent, the character appears to be found more often among animals living in still waters, or it may represent a paedomorphic state (COOMBS *et al.*, 1988). It may not be a sound character to use as an apomorphy of tetrapods, though further study may shed more light on it as an ecological indicator.

19. "Well-ossified pre- and postzygapophyses".

Ichthyostega possesses appreciable zygapophyses, while by contrast *Acanthostega* is now known to lack them almost entirely. It resembles *Crassigyrinus* more closely in this. *Crassigyrinus* is usually regarded as being secondarily aquatic (PANCHEN, 1985), the zygapophyses reduced as a result, so the question arises of whether *Acanthostega* has likewise lost them secondarily or whether it primitively lacked this character found in most other tetrapods.

20. "Ribs that are well developed and turned ventrally".

Unlike *Ichthyostega* which has massive overlapping ribs, *Acanthostega* has short ribs with poorly developed heads. They do not turn ventrally to any significant degree. In this they resemble the ribs of *Greererpeton*, though they are shorter, as far as can be judged. *Greererpeton*, like *Crassigyrinus*, is generally regarded as secondarily aquatic, and as with the zygapophyses, the question is whether *Acanthostega* is primitive in lacking well-developed ribs or secondarily aquatic. *Crassigyrinus* has massive ribs, so small ribs and aquatic habits may not be correlated.

21. "Ribs that extend from the atlas neural arch to caudal 5 or 6".

The distribution of ribs along the axis in *Acanthostega* is incompletely known, though it appears to have atlantal ribs, and immediately post-sacral ones. Cervical and some thoracic ribs are also known.

22. "The loss of all bones above the cleithra".

The anocleithra is now known from Devonian and post-Devonian tetrapods. The first was described from *Tulerpeton* (LEBEDEV, 1984), and PANCHEN & SMITHSON recognised this in their assessment of the character. They cited "dermal pectoral girdle consisting at most of paired supracleithra [*i.e.* anocleithra], cleithra and clavicles". *Acanthostega* is known to possess an anocleithrum (COATES & CLACK, 1991), and an unidentified bone associated with the holotype of *Pholiderpeton scutigerum*, a Coal Measures embolomere (CLACK, 1987), can now be interpreted as an anocleithrum. Figure 2a of GODFREY (1989) shows what appears to be a very similar bone

on a specimen (CMNH 10931) of *Greererpeton* but it needs to be re-examined with this in mind. Presence of the anocleithrum may be more common among the earliest tetrapods than has been previously recognised, but it is certainly a primitive, fish-like character retained by *Acanthostega*. Loss cannot be an apomorphy of tetrapods. However, loss of the remaining supracleithral series and loss of contact between head and dermal pectoral girdle do seem to be a tetrapod apomorphy, which *Acanthostega* shares.

23. "A large, dorsally expanded scapular blade".

This was included with a query by PANCHEN & SMITHSON, while GAFFNEY defined it as "scapulocoracoid relatively larger than dermal shoulder girdle" and included the condition of the endoskeletal girdle as a complex character with the dermal girdle. *Ichthyostega* is described by JARVIK (1980) as lacking a dorsally expanded scapular blade, and we can confirm this description. *Acanthostega* shows a very similar condition, in which the dermal cleithrum is co-ossified with the scapular region of the endoskeletal girdle, and while the junction cannot be certainly identified, it is obvious that the endochondral component was restricted to the more ventral parts of the girdle. The latter bears some similarities to that of *Panderichthys* (VOROBYEVA & SCHULTZE, 1991). This is another character in which *Acanthostega* appears to be primitive, and refutes another postulated tetrapod apomorphy.

24. "A shaft-like cleithrum".

Many of the same comments apply to this character. The cleithra of both *Acanthostega* and *Ichthyostega* are substantial, and both are intimately connected to the endoskeletal girdle, which is relatively smaller than in most other tetrapods.

Next follows a series of characters of the limbs and digits. In GAFFNEY's original list, a single character, "carpus, tarsus and dactyly" was cited, presumably in the belief that these features were co-equal, interdependent, and evolved contemporaneously. PANCHEN & SMITHSON split this complex into six separate characters, while GODFREY used ten differently constituted ones. It is now evident from *Acanthostega* that 'carpus, tarsus and dactyly' is a complex of separate innovations which may be independent, may not have evolved together, and may not all characterize tetrapods.

28. "An olecranon on the ulna".

Acanthostega lacks an olecranon on the ulna. This character may be interpreted as either primitive or a secondary reduction resulting from aquatic adaptation. It will be assessed further below.

PANCHEN & SMITHSON (their character d) cite the following: "radius and ulna (and tibia and fibula) parallel (and primitively independent) ossifications both bearing articular surfaces for the carpus (tarsus) distally". *Acanthostega* lacks obvious articulating surfaces on the ulna distally (COATES & CLACK, 1990).

30. "Distinct digits (dactyly)".

PANCHEN & SMITHSON give a more detailed definition; "manus and pes terminating in a series of separate load-bearing digits, each with a skeleton of articulated phalanges joined proximally to a metacarpal or metatarsal". This definition rules out the digits of *Acanthostega*, which appear not to be load-bearing (COATES & CLACK, 1990). Though both *Acanthostega* and *Ichthy-*

ostega possess distinct digits, they are unconventional tetrapods in the number found on each limb. It was generally assumed that five is the fundamental tetrapod formula, and neither GODFREY nor PANCHEN & SMITHSON specified the number of digits which might be apomorphic for tetrapods. This is fortunate, since it is now known that each of the three described Devonian tetrapod limbs sported more than five (COATES & CLACK, 1990), eight in the case of *Acanthostega*.

31. "At least one pair of sacral ribs".
The sacral ribs and centra of *Acanthostega* and *Ichthyostega* remain unknown.

32. "Long, posterior directed sacral rib, lying against mesial face of ilium".
The sacral ribs of *Acanthostega* and *Ichthyostega* remain unknown. PANCHEN & SMITHSON combine these two characters (31, 32) as their character 1 and extend it to "ilium of pelvic girdle on each side directly connected to one or more sacral vertebrae by specialised sacral ribs". It should be noted that in many early tetrapods, the exact nature of the connection between the sacral rib and the ilium is poorly understood, and in many cases seems to have been formed only by soft tissue rather than by bony articulations.

33. "Pubis, ischium and ilium in pelvis".
Although *Acanthostega* shows no sutures in the pelvic plate, these three regions are assumed to be represented, as they are in *Ichthyostega*.

34. "An anterior and posterior tongue-like projection on either side of the supra-acetabular buttress".
Acanthostega has no anterior tongue-like projection (COATES, in prep.).

39. "Wrist and knee joints hinge-like, elbow and ankle rotatory".
PANCHEN & SMITHSON separate this into two characters: g) "wrist joint incorporating the radius and forming a hinge" and i) "rotatory ankle joint incorporating the tibia". The wrist joint of *Acanthostega* is unlike that of any other known tetrapod, and its range of movement was probably very limited. The ankle-joints of both *Acanthostega* and *Ichthyostega* are very similar to each other, and as with the wrist-joint, were very limited in movement. It is highly improbable that they were rotatory (COATES & CLACK, this volume).

PANCHEN & SMITHSON also give an additional tetrapod apomorphy, concerning the pattern of the dermal cheek bones. *Acanthostega* displays this pattern, with a jugal – quadratojugal suture separating squamosal and maxilla, but is has now also been reported in on one side of one specimen of *Panderichthys* (VOROBYEVA & SCHULTZE, 1991). *Acanthostega* also shares several characters of the lower jaw with most other tetrapods, including an anterior coronoid – pre-splenial suture, and a surangular contribution to the adductor fossa (CLACK, 1988). In both of these characters, *Ichthyostega* shows the non-tetrapod condition (JARVIK, 1980). These characters will be described and further tetrapod apomorphies of the lower jaw will be discussed in a forthcoming paper by one of the current authors (J. A. C.) and P. E. AHLBERG. Early tetrapods also share characters of the dermal armour, in terms of the form and distribution of scutes, which appear to be apomorphic, but which have yet to be formally defined. *Acanthostega* and *Ichthyostega* (pers. obs.) share these characters.

Of the 41 characters listed by GODFREY (1989) as tetrapod apomorphies, *Acanthostega* exhibits 26 unequivocally. It also shares at least four additional characters not listed by GODFREY, making a total of 30 out of 45. Counted thus, informally speaking and noting the caveat above, this makes it just two-thirds a tetrapod. Of the remaining characters, four are unknown or uncertain not only in *Acanthostega* but in many other early tetrapods, and one may be a poor taxonomic character. In the remaining eight characters, *Acanthostega* shows the non-tetrapod, presumed plesiomorphic condition. Some of these are also found in *Ichthyostega*. Consideration of these characters will follow.

PLESIOMORPHIC CHARACTERS OF *Acanthostega*

Acanthostega shows a suite of characters in which it is plesiomorphic for tetrapods, some of which it shares with *Ichthyostega* and others in which it is unique among tetrapods. Other apparently plesiomorphic characters could be secondarily acquired as a result of aquatic habits, rather than retentions from a primitively aquatic state. Examination of these characters may help to polarise them, so that they can be used in subsequent analyses of the relationships of tetrapods, the sequence of acquisition of tetrapod characters and the evolution of terrestriality.

Acanthostega shares several apparently plesiomorphic characters with *Ichthyostega* in addition to those mentioned above. One character complex concerns the braincase, and has no obvious bearing on whether the animals were aquatic or not. Though the preserved braincases of the two genera are very different in most respects, they both share the plesiomorphic condition of a notochordal basi-occipital, and the ventral cranial fissure, though sutured, remains exposed in the adult by retention of a short parasphenoid (CLACK, 1994). This character has featured in analyses of the relationships of tetrapods to fishes (ROSEN *et al.*, 1981; PANCHEN, 1985) in which it has been argued that tetrapods and lungfishes were similar in having a long parasphenoid which sealed the ventral cranial fissure. It is now clear that in the earliest tetrapods parasphenoid and basi-occipital were not firmly united, even in Carboniferous and Permian genera (CLACK & HOLMES, 1988; CLACK, 1994). It is important to characterize the plesiomorphic condition of any group in an analysis of its relationships (SCHULTZE, 1987).

The second character complex concerns the tail, and suggests that the animals were predominantly aquatic. Both retain lepidotrichia in the tail-fin, supported by a series of radials, though in *Acanthostega* the lepidotrichia were relatively much longer than in *Ichthyostega*. As described above, both also share characters of the pectoral girdle including the proportions of the endoskeletal girdle (which is probably plesiomorphic) and the co-ossification of that with the cleithrum (whose polarity is difficult to evaluate). Neither of these is obviously an adaptation for aquatic or terrestrial living.

Another suite of characters in which *Acanthostega* appears to be uniquely primitive concern the retention of a well-ossified, grooved hyobranchial skeleton and a post-branchial lamina of the cleithrum. In both these, *Acanthostega* is remarkably fish-like (COATES & CLACK, 1991). We have interpreted them as indicating that the animal was primarily and primitively aquatic, but alternatively, they could be non-functional plesiomorphies.

Characters in which *Acanthostega* is fish-like, but which have no obvious connection with habit include: retention of the anocleithrum; remarkably fish-like vomers and palatal dentition (CLACK, 1994); lack of suture between the prearticular and any but the most anterior splenial (AHLBERG & CLACK, in prep.); and the proportions of the radius and ulna (COATES & CLACK, 1990). In the latter, it most closely resembles the osteolepiform *Eusthenopteron*, and is unlike all other known tetrapods including *Ichthyostega*.

The remaining characters from the list in which *Acanthostega* does not show the apomorphic tetrapod condition could all be interpreted as aquatic adaptations. These include: the lateral line canals carried in tubes in the bone; lack of zygapophyses; short, straight ribs; no olecranon on the ulna; and paddle-like limbs with non-rotatory ankle joint. *Acanthostega*, though possessing indisputable digits, is unusual in having eight per limb which appear to form an effective paddle rather than a load bearing appendage. In addition, *Acanthostega* possesses a plate-like, relatively heavy stapes (CLACK, 1989) which has been interpeted as the basic condition for tetrapods, but which may be an aquatic adaptation.

Acanthostega, PRIMITIVELY OR SECONDARILY AQUATIC?

There can be little doubt that *Acanthostega* was an aquatic animal. Taking into account all its fish-like features, we get a consistent picture of a swamp-dwelling air-gulper, living and feeding in water. The question is, was it a transitional form retaining many characters of its fish-like ancestor but not yet having evolved the full complement of tetrapod characters, or a specialized form derived from a more terrestrial ancestor which nevertheless retains many plesiomorphic features? It could also be that at this early stage of tetrapod history, these two possibilities are not so far removed from one another.

We have argued elsewhere (COATES & CLACK, 1990, 1991) that the form of the limbs and retention of the fish-like gill skeleton indicate an animal which was primitively aquatic. Our study of the limbs suggested that they were more likely to have evolved for use in water rather than on land. They seem plausible as paddles but not as load-bearing legs, and evidence from developmental biology (SHUBIN & ALBERCH, 1986) suggests that more than five digits, as found in *Acanthostega*, *Ichthyostega* and *Tulerpeton*, more likely represent a primitive condition, with the pentadactyl limb derived by reduction.

We followed this by discovery of the gill skeleton, which augmented the picture of an aquatic gill-breather. Many of the fish-like features of *Acanthostega* accord with this idea. However, we can be accused of some circularity of reasoning. *Acanthostega* manifestly exhibits many characters of tetrapods some of which are usually taken to be associated with evolution of terrestriality and loss of gill-breathing. It has lost the operculogular series from the skull, bones which are associated with use of gills in fishes. More compelling still is the presence of a large pelvic plate, which is usually taken to be correlated with support of the hind-limbs in the characteristic rear-limb propulsion of tetrapods. It seems hard for some to accept the evolution of the pelvis separate from the evolution of walking.

We counter these arguments thus. The two more derived genera of modern lungfishes, swamp-dwelling air-gulpers, have lost those bones of the skull associated with gill-breathing,

and have a soft opercular wall. Although *Acanthostega* has a pelvis, we cannot yet be sure that it was attached to the vertebral column; certainly there is no evidence of a bony connection. We can put forward some scenarios (untestable) for why a pelvis might have evolved. (Risking levity, we suggest: to provide support for hindlimbs during underwater propulsion and rapid changes of direction; during digging of nests or burrows; for use in amplexus.) What we find difficult to accept are, on the one hand, retention of the tail-fin with lepidotrichia more extensive than those of *Ichthyostega* if the animal had a more terrestrial ancestor, and on the other hand, the idea that the primitive, fish-like proportions of the radius and ulna should have been re-evolved in *Acanthostega* when all other secondarily aquatic tetrapods retain normal tetrapod proportions there.

These arguments are admittedly subjective, both sides based on prejudices and preferences. Are there more objective means for judging the issue? For reasons outlined above, simply counting characters is unsatisfactory. Perhaps the problem should be approached from a different point of view. Assuming tetrapods evolved from fish or fish-like ancestors, their origins would be from aquatic animals. The plesiomorphic condition would be for the earliest tetrapods to be aquatic. in other words the null hypothesis should be that the earliest tetapods were aquatic, unless this can be refuted by good evidence. To argue that *Acanthostega* was secondarily aquatic and that the gill-skeleton and post-branchial lamina were non-functional retentions seems less than parsimonious. Given its complement of primitive and fish-like characters, it is simplest to argue that it was exactly that.

This begs the question of what would constitute good evidence of terrestriality. Load-bearing wrists and ankles and their associated movements, with perhaps reduction in the number of digits to five or fewer may be the best, though this would be difficult to establish in many fossil tetrapods.

This problem is exacerbated by the transitional nature of the environments in which these early tetrapods presumably lived, neither fully aquatic, nor fully terrestrial, but vegetation-choked swampy marginal habitats. It is not surprising therefore that we find difficulty in distinguishing aquatic from terrestrial organisms.

THE ACQUISITION OF TETRAPOD CHARACTERS

Acanthostega and *Ichthyostega* tell us a number of things about the sequence of acquisition of tetrapod characters. For example, we can infer that loss of most of the supracleithral series occurred before consolidation of the braincase and development of a true occiput. Development of the humerus into the form characteristic of tetrapods occurred before the development of the typical tetrapod scapulocoracoid.

If we are right in our assessment of *Acanthostega* as a primitively aquatic tetrapod, we can make other inferences. Loss of the gulars, submandibulars and separate bony operculars occurred before loss of gill-breathing; digits evolved before the more typical tetrapod joints of wrists and ankles; legs and pelvis arose before walking on land.

On the other hand we may find that further discoveries may complicate the issue. We already know that *Ichthyostega* is more primitive than *Acanthostega* in some respects such as the form

of the lower jaw, while *Acanthostega* is more primitive than *Ichthyostega* in others such as the form of the radius and ulna and the post-branchial lamina of the shoulder girdle. Fragmentary remains of tetrapods from the Devonian of Scotland (AHLBERG, 1991) possibly indicate animals that had tetrapod-like hind limbs and girdles, but fish-like humeri, while some from Latvia have more fish-like lower jaws with tetrapod-like dermal pectoral girdles (AHLBERG *et al.*, 1994).

Acquisition of tetrapod-like characters may exhibit mosaic evolution comparable to that evident during the transition from mammal-like reptiles to mammals (KEMP, 1982). As with mammals, we may have to define tetrapods on possession of a single, more or less arbitrarily chosen character as the transition becomes better documented. It will have to be a skeletal character. Functional assumptions such as 'breathing through nasal openings and walking on feet' (SCHULTZE, 1991: 30) will not be appropriate and may well not have been true of the earliest tetrapods.

PANCHEN & SMITHSON (1987) express a commonly accepted view when they state (p. 366) : "It is agreed by GAFFNEY, ROSEN *et al.* and ourselves, together with numerous previous workers, that the carpus, tarsus and dactyly of tetrapods is their most important autapomorphy". As we have seen, this is not a single apomorphy. Dactyly may have arisen before a true carpus or tarsus. Dactyly appears to be produced as a result of developmental processes common to all sarcopterygians (SHUBIN & ALBERCH, 1986) and may prove difficult to define as more transitional forms are discovered. A sarcopterygian with segmented post-axial radials could be said to exhibit dactyly. Transitional forms can be envisaged with digits on one pair of limbs (likely the hind) but not on the other or in which the limbs bore digits but in which the supracleithral series was still present.

At the present time, the presence of digits is, in practice, the single character which we use to define tetrapods. Had *Acanthostega* possessed unsegmented post-axial radials with or without lepidotrichia (and given the proportions of radius and ulna we were almost expecting this), we should have hesitated to call it a tetrapod. Nevertheless, we should like to point out the potential inadequacies of this character for the future. Choice of another will depend upon what is shown among further fossil forms about the sequence of acquisition of characters. For example, if the supracleithral series were lost only after development of digits, loss of this series might be seen as more significant. On the other hand we may view what appears to be a 'neutral' or not obviously adaptive character, like consolidation of the snout bones, as a more useful choice. Then again, it may become clear that the enlarged pelvic plate is correlated with development of hind-limbs with ankles and digits before the fore-limb became recognisably tetrapod, in which case the pelvic plate may be the most significant tetrapod character. It seems that the contrast in the structure of the pelvis of fishes and tetrapods is one of the greatest between them, and even the homologies of the elements are disputed (PANCHEN & SMITHSON, 1990).

The advantages of an alternative and completely contrasting method were recently aruged for by GAUTHIER *et al.* (1988). This method eliminates the difficulties of a definition based on key characters, utilising instead a phylogenetic or node-based definition. Thus according to this definition, the term "Tetrapoda" is defined as that clade above the node represented by the common ancestor of modern amniotes and anamniotes. This definition has subsequently generated much discussion (e.g. LUCAS, 1992; ROWE & GAUTHIER, 1992; DE QUEIROZ & GAUTHIER, 1992; PATTERSON, 1993) but the current paper is not the place to consider its relative merits. Work

in progress has considered the position of *Acanthostega* and other early tetrapods under this regime, and will be published with a description of the postcranial anatomy of *Tulerpeton* by LEBEDEV & COATES.

The origin of tetrapods has long been a source of speculation and debate, not less so now, but as we discover new fossils our speculations and hypotheses have a sounder base, they can take off in new directions and we can perhaps ask more readily answerable questions. We hope that discovery and description of *Acanthostega* is just the beginning.

TABLE 1. — Tetrapod apomorphies and *Acanthostega*. Numbers from GODFREY, 1989. G-number given in GAFFNEY, 1979 (including Neotetrapod apomorphies). PS-, letters given in PANCHEN & SMITHSON, 1987: 369 ??, condition unknown or uncertain in *Acanthostega*. *Italics*, character absent in *Acanthostega*.

*Liste des apomorphies des tétrapodes et d'*Acanthostega. *Les nombres sont tirés de GODFREY, 1989. G- nombre donné dans GAFFNEY, 1979 (incluant les apomorphies des néotétrapodes). PS-, lettres données dans PANCHEN & SMITHSON, 1987 : 369 ??, Condition inconnue ou incertaine chez* Acanthostega.

G4	PSa	1. Single pair of nasal bones;
		2. Parietals wider than frontals;
		3. Postparietals shorter than parietals;
		4. Tabular tubercle on occipital surface;
		5. Jugal forms at least half of lower orbit margin;
		6. Medial abutment of pterygoids below cultriform process;
G13		7. *No operculum*;
		8. No median gular;
		9. No submandibulars;
		10. 'Peg and socket' basal articulation;
G6	PSc	11. Fenestra ovalis??;
G5	PSb	12. Stapes?;
		13. *Unossified laterosphenoid?*;
		14. Sphenethmoid Y-shaped anteriorly, V-shaped posteriorly;
		15. Loss of tusk and replacement pair on at least one coronoid;
G15		16. *Some lateral lines in canals, not tubes in the bone lower mandible;*
		17. Dermal sculpturing characteristic pits and ridges;
		18. Differentiated atlas and axis, with atlas arch halves, and relatively massive axis arch;
		19. *Well-ossified zygapophyses;*
G11		20. Ribs well-developed and turned ventrally;
		21. Ribs extend from atlas to caudal 5 or 6;
G8	PSj	22. *Loss of all bones above the cleithrum;*
	PSk	23. *Large dorsally expanded scapular blade;*
		24. *Shaft-like cleithrum;*
		25. Large interclavicle;

		26. Preaxial keel on humerus;
		27. Rectangular entepicondyle;
		28. *Olecranon on ulna;*
G7	PSe	29. Carpal and tarsal elements;
G7	PSf	30. Digits;
G9/10	PSl	31. At least one pair of sacral ribs ??;
G9	PSl	32. Long posteriorly directed sacral rib, lying against mesial face of ilium ??;
G9/10	PSm	33. Pubis, ischium and ilium in pelvis;
		34. Anterior and posterior projection on either side of supra acetabular buttress;
		35. Laterally directed acetabulum;
		36. Puboischiadic plate pierced by foramina;
		37. Well-developed adductor crest on femur;
		38. Two canals pierce distal end of femur;
	PSg, h&i	39. *Wrist and knee joints hinge-like, elbow and ankle rotatory;*
	PSi	40. Articular condyle on distal end of tibia;
		41. Intermedium articulating directly with tibia and fibula;

Other tetrapod apomorphies present in *Acanthostega*.

Autres apomorphies de tétrapodes présentes chez Acanthostega.

PSn	Dermal cheek pattern (PANCHEN & SMITHSON, 1987);
	Anterior coronoid / presplenial suture (CLACK, 1988);
	Surangular contribution to adductor fossa (CLACK, 1988);
	Form and distribution of dermal scutes.

Other tetrapod apomorphies absent in *Acanthostega*.

Autres apomorphies de tétrapodes absentes chez Acanthostega.

	PSd	Radius and ulna both bearing articular surfaces for the carpus distally;
G12		Persistent notochord excluded from braincase;
G14		Median bony fin supports with lepidotrichia absent;
G16		Ethmosphenoid and parachordal (otico-occipital) portions of braincase solidly fused in adult, not separated by a suture.

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ROMER's gap: tetrapod origins and terrestriality

by Michael I. COATES and Jennifer A. CLACK

Abstract. — New data derived from recent discoveries of Devonian tetrapods necessitate a revision of frequently expressed palaeoecological and morphogenetic scenarios concerning the fish-tetrapod transition. Many current hypotheses link tetrapod origin closely to terrestrialisation in a theleological explanation of tetrapod evolution. In contrast, ROMER emphasised the separation of these two events. ROMER's view is corroborated by new data that indicates that tetrapods were originally aquatic and preceded the earliest known terrestrial fauna by ~ 25 mya. Three varied Upper Devonian tetrapods are now known in detail: *Acanthostega*, *Ichthyostega*, and *Tulerpeton*. New reconstructions of *Acanthostega* and *Ichthyostega* are presented, including preliminary details of the acanthostegid vertebral column, pelvic girdle, and hind limb. *Acanthostega*, anatomically closest to osteolepiform fish, is preserved in active fluvial channels. *Ichthyostega* is re-interpreted as having a seal-like postcranial skeleton; *Tulerpeton*, resembling more recent Carboniferous tetrapods, is found in shallow marine sediments. There is little support for an exclusively freshwater tetrapod origin. Comparison of acanthostegid anatomy with *Panderichthys*, and quantified changes between small and large specimens of *Eusthenopteron*, suggest dissociated heterochronic changes in early tetrapod evolution. Early tetrapod remains coincide with the Frasnian-Famennian extinction, which included massive depletion of the oxygen-content of marine surface-waters. High faunal turnover, the adaptive advantage conferred upon air-breathers, and the possibility that early tetrapods occupied marine environments, suggest that this extinction event facilitated the evolutionary radiation of early or near-tetrapods.

Keywords. — Devonian tetrapods, aquatic origin, heterochrony, Frasnian-Famennian extinction, marine environment.

La lacune de ROMER : les origines des tétrapodes et l'adaptation à la vie terrestre

Résumé. — De nouvelles données tirées des découvertes récentes sur les tétrapodes dévoniens nécessitent une révision des scénarios les plus couramment établis sur la paléo-écologie et la morphogenèse de la transition entre les poissons et les tétrapodes. Les hypothèses courantes rattachent l'origine des tétrapodes à une terrestralisation selon une explication théologique de l'évolution des tétrapodes. À l'inverse le point de vue de ROMER est corroboré par une nouvelle donnée qui indique que les tétrapodes étaient à l'origine aquatiques et précédèrent les premières faunes terrestres de 25 millions d'années. Trois tétrapodes du Dévonien supérieur sont connus en détail : *Acanthostega*, *Ichthyostega* et *Tulerpeton*. De nouvelles reconstitutions d'*Acanthostega* et d'*Ichthyostega* sont présentées, dont des détails préliminaires de la colonne vertébrale, de la ceinture pelvienne et du membre postérieur d'*Acanthostega*. Ce dernier est anatomiquement proche des ostéolépiformes, il est conservé dans des sédiments de chenaux fluviaux, le squelette postcrânien d'*Ichthyostega* est réinterprété à la lumière de celui des phoques ; *Tulerpeton*, trouvé dans des sédiments marins de faible profondeur, ressemble plus aux tétrapodes carbonifères, plus récents. Une origine dulçaquicole des tétrapodes est peu étayée. La comparaison de l'anatomie d'*Acanthostega* avec celle de *Panderichthys* ainsi que les changements quantifiés entre des spécimens petits et grands d'*Eusthenopteron* suggèrent une hétérochronie dissociée dans l'évolution des premiers tétrapodes. L'extinction du Frasnien-Famennien coïncide avec la découverte de restes des premiers tétrapodes, laquelle est accompagnée d'une baisse importante de la concentration en oxygène de la tranche d'eau supérieure des mers. La conjugaison d'un renouvellement de faune, de l'avantage adaptatif que constitue la respiration aérienne et de la possibilité que les premiers tétrapodes aient occupé un environnement marin suggèrent que cette extinction a pu faciliter la radiation évolutive des premiers tétrapodes.

Mots-clés. — Tétrapodes dévoniens, origine aquatique, hétérochronie, extinction du Frasnien-Famennien, environnement marin.

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INTRODUCTION

A wealth of new data on early tetrapod fossils from the Upper Devonian of Greenland, Russia, and Scotland, allow us to reassess frequently expressed theories of tetrapod origin and terrestriality. The phylogenetic implications of these data are discussed elsewhere in this volume (CLACK & COATES). Phylogenetic analysis has to precede discussion of palaeobiological scenarios, although the latter may subsequently help to resolve systematic problems (e.g. CAMPBELL & BARWICK, 1988). Many hypotheses of the fish-tetrapod transition can be classified as either palaeoecological or morphological transformation scenarios. In this paper these not entirely distinct aspects of tetrapod evolution will be reviewed briefly and separately. Biogeographical theories of the location of the fish-tetrapod transition are not discussed in detail, although recent finds from Scotland (AHLBERG, 1991a) and Latvia (GEE, 1991), suggest that early or near-tetrapod distribution may be broader than has been proposed recently (e.g. LONG, 1990a).

PALAEOECOLOGICAL SCENARIOS, PAST THEORIES

Most palaeoecological models of early tetrapod life have been influenced by the works of BARRELL (1916) and WATSON (1926). BARRELL proposed that tetrapods arose in fresh waters, from fluviatile fishes during the Lower Devonian. The environment consisted of a warm climate and seasonally drying river plains remote from continental margins, where terrestrial locomotion and air breathing conferred considerable advantages upon the proto-tetrapods. WATSON's contrasting scenario consisted of swampy pools enclosed by endless (Carboniferous) coal forests within which large embolomerous anthracosaurs such as "*Eogyrinus*" (*Pholiderpeton*, CLACK, 1987), swam using their long, deep tails, and whose small limbs were regarded as entirely unsuited for terrestrial use. Seasonal drought prompted terrestrial forays in search of new habitats, which WATSON compared to the passage of extant eels from one ditch to another; a significant limbless feat.

ROMER effectively combined both hypotheses in what has come to be the prevailing tetrapod-origin scenario (summarised in 1958, and references therein) set in BARRELL's Devonian red-beds rather than WATSON's Carboniferous coal-measures. SAVE-SODERBERGH's (1932) discovery of Upper Devonian (Famennian) tetrapods (*Ichthyostega*, *Ichthyostegopsis*, and *Acanthostega*, JARVIK, 1952) enabled ROMER to couple these to WATSON's "raison d'être" (ROMER, 1958: 365) for pool to pool transmigration. However, limbs were argued to have evolved specifically as an adaptation enabling aquatic animals to migrate from drying pools to those of a less ephemeral nature. ROMER's was, therefore, a paradoxical scenario, in which limbs evolved for terrestrial use, in order to facilitate an extended aquatic lifestyle. The first fully terrestrial vertebrate faunas were envisaged to occur much later, at the Permo-Carboniferous boundary, concomitant with the origin of amniotes and abundant terrestrial food resources.

Many of the contemporary criticisms of ROMER's scenario were based, in part, upon a misreading which ignored his emphasis upon the huge temporal gap (65 mya) between the earliest tetrapod skeletal remains, and the earliest terrestrial vertebrate faunas. For example, GUNTER (1956) and INGER (1957) accused ROMER of arguing for a saltatory tetrapod origin, within the

instant of a catastrophic drought. They and others, including ORTON (1954) and GOIN and GUNTER (1956), also argued that the vertebrate inhabitants of drying pools today huddle in the remaining moisture, and disperse only if the surrounding environment is sufficiently wet. INGER demanded continuously humid conditions for the evolution of tetrapods and terrestriality, whereas ORTON argued for the origin of the tetrapod limb as a fossorial device, to assist aestivation rather than as an aid for dispersal. GUNTER provided the broadest of functional scenarios; it is probably the earliest argument for a fully aquatic origin for the tetrapod limb. In support of this, GUNTER listed numerous examples of actinopterygians which walk under the water, a theme returned to by EDWARDS (1989). This provided an incipient stage between fins consisting mostly of dermal bone, and endoskeletally supported, highly muscular tetrapod limbs. GUNTER envisaged aquatic ancestral tetrapods being marginalized by larger predators (BERRY's, 1918, *in* GUNTER, 1956) ("swarming hordes of ganoid pirates"), and only after refuge was found in shallows were limbs and girdles evolved to cope with terrestrial loads. This model circumvented the progressionist trap in which phrases such as the "invasion" or "colonization of dry land" implied orthogenetic evolutionary processes. GUNTER cannily differentiated limbs from fins by the absence of lepidotrichia, but his support for EATON's (1951) hypothesis that fin-ray loss provided an adaptive premium during time spent out of water, returned to the orthodox view of limb origination as inextricably linked to terrestrialisation. ROMER's scenario was never considered to be mutually exclusive of GUNTER's, but related more closely to the subsequent fine-tuning of limb development.

ROMER's 1958 summary provided an effective reply to many of these criticisms (but neglected GUNTER's views on the aquatic origin of limbs, and marginalization). ROMER's scenario was based upon a series of important assumptions: that the Devonian red-beds were deposited under semi-arid conditions; that although forests had developed by the late Devonian, they did not constitute evidence of a continuously moist climate. If any representative Mid- to Upper Devonian fish fauna was examined, and ROMER used the Escuminac assemblage as his preferred example, 95% of any "catch" consisted of fish with lungs (lungs having a major adaptive value during conditions of seasonal drought); the potential food supply on land was meagre, and this delayed the development of the first terrestrial vertebrate faunas. The first true land dwellers were concluded to be *Eryops*-like, living at the Carboniferous-Permian boundary, after the origin of insects, which provided necessary terrestrial food.

Ecophysiological arguments were also applied to the water-land transition, with especial reference to osmoregulation (summarized in LITTLE, 1990). Physiological constraints may have determined whether the earliest terrestrial vertebrates emerged from the fresh waters of BARREL's continental flood plains, or from the salt waters of continental margins, estuaries and lagoons. The ecophysiological case derives from the evidence of blood composition and osmotic pressure: most amphibians are hypo-osmotic, and unable to tolerate rising osmotic pressure from dessication or rising salinity in the external medium. They are considered to be osmotic "regulators" rather than "tolerators", and only the development of a less permeable skin and larger size enabled the colonization of a dessicating environment. Amphibians, and therefore the earliest tetrapods, were concluded to have evolved in fresh waters. Furthermore, inhabitants of oxygen depleted, warm ephemeral or swampy freshwater habitats would already have been subjected to intense selective pressure to evolve aerial breathing, a key physiological prerequisite for the evolution of terrestriality. THOMSON's (1980) palaeoecological review of Devonian sarcopterygians, which

included the closest known relatives of early tetrapods, disagreed. Only very few, mostly Late Devonian taxa, were restricted to freshwater deposits, and early tetrapods were associated with fishes also known to occur in marine sediments. THOMSON concluded that most sarcopterygians were anadromous, living in the sea but entering fresh waters to breed and feed in the brackish shallows of estuaries and coastal lagoons. These migrations may have been seasonal, and tied closely to the development of the first continental ecosystems. With these data, THOMSON asked if the first tetrapods could, unquestionably, be assumed to be fully freshwater animals. Support for this hypothesis has been supplemented by BRAY's (1985) suggestion that the ionic compositions of Devonian marine and fresh waters were far less distinct than today's equivalents. LITTLE (1990: 181), however, concluded that in contrast to the freshwater habitat, there was difficulty in identifying the selection pressures for airbreathing in a marine environment.

Until 1986, the earliest available glimpse of tetrapod evolution remained that of *Ichthyostega* with its fish-like tail trailing symbolically in the water (MILNER *et al.*, 1986). Almost all waterland, fish-tetrapod hypotheses centred upon *Ichthyostega*, despite this being a generic name applied to a composite reconstruction (JARVIK, 1952; 1980; BJERRING 1988, 1989), derived from the five species erected by SAVE-SODERBERGH (1932). The validity of SAVE-SODERBERGH's specific diagnoses, based upon variations in dermal skull proportions and composition, has never been reviewed. JARVIK's statement that "*Ichthyostega* in many regards is more specialized than later appearing tetrapods and is far from being some kind of prototetrapod" (1980: 222) has been mostly ignored. However, the sum of the data available in 1986, and discoveries reported since then, amount to a considerable improvement upon the evidence available to ROMER, pre-1960.

Many of these discoveries are included in MILNER *et al.*'s (1986) review, including a summary of the earliest known terrestrial vertebrate fauna: East Kirkton, Scotland (WOOD *et al.*, 1985; ROLFE *et al.*, 1993), with an estimated age of 338 mya (Scottish Upper Visean). Knowledge of Devonian tetrapods has improved similarly. Tetrapod trackways have been described from the Upper Devonian (probably Frasnian) (WARREN & WAKEFIELD, 1972) and much less certainly, the Lower Devonian (WARREN *et al.*, 1986) of Australia, and the Middle Devonian (Givetian) of Scotland (ROGERS, 1990). CAMPBELL & BELL (1977) described a possible tetrapod jaw from the Upper Devonian of Australia (*Metaxygnathus*), and LEBEDEV (1984, 1985, 1990a) partially described the articulated appendicular and incomplete axial skeleton of a new tetrapod *Tulerpeton*, from the Upper Devonian Andreyevka-2 locality of the Tula Region, Russia (see LEBEDEV, 1990b, for a detailed faunal review). LEBEDEV & CLACK (1993) have now recognised the presence of at least two tetrapods among the cranial fragments ascribed to this material, but the articulated postcranial type-material (currently being redescribed by LEBEDEV & COATES) remains sufficiently well preserved to be diagnostic, and displays significant affinities with PANCHEN & SMITHSON's (1988) reptiliomorph ramus. In 1987, an Anglo-Danish expedition to East Greenland collected new specimens of *Ichthyostega*, and *Acanthostega* (PANCHEN, 1988), and the sedimentological context of Devonian tetrapod material was recorded *in situ* (BENDIX-ALMGREEN *et al.*, 1990). The acanthostegid material has already yielded important information about the evolution of the tetrapod middle-ear (CLACK, 1989), the structure of the earliest known limbs (COATES & CLACK, 1990; COATES, 1991), and the presence of internal gills (COATES & CLACK, 1991). Much of this information has been obtained from what is probably the most complete known specimen

of a Devonian tetrapod. Most recently, AHLBERG (1991a) has described tetrapod or near-tetrapod fragmentary fossils from the Upper Devonian (Frasnian) of Scotland, and, with LEBEDEV & LUKSEVICS, found similarly aged tetrapod-like specimens in Latvia (GEE, 1991).

Studies of tetrapod-like fish have paralleled advances in our knowledge of fish-like tetrapods. Criticisms of ROSEN *et al.*'s (1981) proposal of dipnoans as the tetrapod sister-group have been elaborated elsewhere (e.g. PANCHEN & SMITHSON, 1987; CAMPBELL & BARWICK, 1984, 1988). In this article a sister-group relationship between osteolepiforms and tetrapods is accepted (e.g. SCHULTZE, 1987 [including rhizodonts and panderichthyids plus tetrapods in a trichotomy with osteolepiforms]; AHLBERG, 1991b), wherein members of the family Panderichthyidae (VOROBYEVA, 1968) are considered to be the closest relatives of tetrapods. Recent descriptions of panderichthyids include *Elpistostege watsoni*, from the Upper Devonian (Frasnian), Escuminac Formation, of Canada (SCHULTZE & ARSENAULT, 1985) and *Panderichthys rhombolepis*, from the Upper Devonian (Frasnian) of Latvia (VOROBYEVA & SCHULTZE, 1991).

We now know that by the end of the Devonian many more organisms had made the transition to the terrestrial environment than ROMER perceived. SHEAR (1991) summarises current research into the earliest terrestrial ecosystems. By the end of the Devonian, architecturally modern forests and other plant communities had become established; nearly all the main clades and adaptations (excluding flowers and fruit) had emerged. Well developed litter faunas had evolved, consisting of small detritivorous and predatory arthropods, and insects had emerged from the myriapod-hexapod lineage. One response to the foregoing review might be simply to shunt ROMER's scenario a few tens of millions of years further into the past, but this fails to disentangle the tetrapod and terrestriality problem any further, and accepts SHEAR's curious statement that the skeletons of the earliest tetrapods (meaning *Ichthyostega* and *Acanthostega*) are "already quite modern".

NEW DATA

Even if all specimens that contributed to the reconstruction of *Ichthyostega* derive from a single species, several important regions of the skeleton remain unknown. These include the presence or absence of an atlas-axis complex, the structure of the manus, the form of the sacral region and the post-sacral insertion of the tail. The hind limb is now known to be paddle-like rather then leg-like, and septa- rather than pentadactylous (COATES & CLACK, 1990). As in most fishes, the humerus is significantly larger than the femur (also noted in SCHMALHAUSEN, 1968, and BJERRING, 1988), and in contrast to the paddle-like hind limb, the massive forelimbs are permanently flexed at the elbow, with short radii articulating entirely beneath the anterior humeral flanges. Although the tail retains fish-like lepidotrichia, it appears to be hypocercal, and shorter than those of other tetrapods. The broad, overlapping ribs were interpreted by JARVIK (1980) as conferring stiffness to an otherwise fish-like trunk. Corroborative evidence for this interpretation is provided by an analysis of the structure and function of the remarkably similar ribcage of the arboreal, two-toed anteater, *Cyclopes didactylus*, (Fig. 1B). JENKINS (1970) describes how, with relatively little enhancement of the musculature, intercostal contraction effectively locks the overlapping, expanded ribs together into a stiff, barrel-like form. This trick is utilised by *C.*

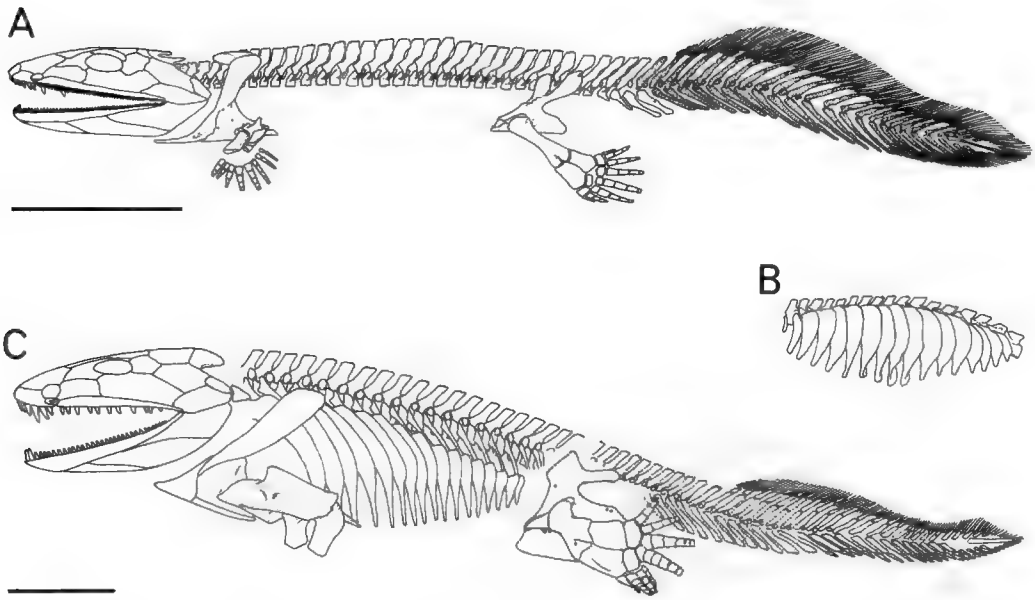

FIG. 1. — Skeletal reconstructions of Devonian tetrapods from East Greenland.
A. *Acanthostega gunnari*: provisional restoration omitting ribs and gastralia. Stippled region of tail adapted from JARVIK's (1980, Fig. 156) restoration of tail of *Ichthyostega*, although lepidotrichia are lengthened to conform with relative proportions of incompletely prepared acanthostegid tail specimens. B. Expanded thoracolumbar ribs of *Cyclopes didactylus* (sternum omitted) (from JENKINS, 1970, Fig. 1A). C. New restoration of *Ichthyostega* sp., adapted principally from JARVIK (1980, Fig. 170). Unknown regions of postcranial anatomy omitted. Upper jaw dentition adapted from *Ichthyostega eigili* (SAVE-SODERBERGH, 1932, Fig. 7); hindlimb from COATES & CLACK (1990; Fig. 1d-f). Scale bars = 10 cm

Reconstitutions du squelette des tétrapodes dévoniens de l'est du Groenland.
A. Acanthostega gunnari, *reconstitution partielle, les côtes et les gastralia manquent. La région caudale est adaptée de celle d'* Ichthyostega *(d'après* JARVIK, *1980, Fig. 156) bien que les lépidotriches aient été allongés en raison de leurs proportions relatives sur la région caudale de spécimens incomplètement préparés d'*Acanthostega gunnari. *B. côtes thoracolombaires de* Cyclopes didactylus *(sans le sternum) d'après* JENKINS *(1970, Fig. 1A). C, nouvelle reconstitution d'*Ichthyostega eigili *(*SAVE-SODERBERGH, *1932, Fig. 7), membre postérieur d'après* COATES & CLACK *(1990, Figs., 1d-f). Échelle = 10 cm.*

didactylus to suspend itself horizontally from a branch, obtaining purchase with only its hind limbs and prehensile tail, while extending its forelimbs laterally in a defensive posture, or grasping for a nearby twig. This demonstrates the extraordinary axial ridgidity which may be obtained with a set of overlapping ribs, and challenges SCHMALHAUSEN's (1968) inference from vertebral morphology that the spinal musculature was differentiated sufficiently to resist terrestrial loads unaided, with expanded ribs functioning principally as an insertion for strongly developed serrate muscles, anchoring the pectoral girdle.

The conventional restoration of *Ichthyostega* as a vaguely urodele-like quadruped fails to explain the presence of these unusual anatomical features. However, a group of extant aquatic tetrapods exhibits a number of unexpected similarities: the Pinnipedia (seals, sea lions and walruses). In these the pectoral limbs function as an anterior prop, while the pelvic limbs serve as propulsive paddles and rudders. The humeral and femoral proportions are extremely similar to

those of *Ichthyostega*. In *Mirounga leonina*, the elephant seal, the femoral length is less than two thirds of the humeral length. The hind limbs have the shortest toes within the middle of the digital arch, paralelling the tiny digit within the digital arch of the ichthyostegid hind limb. The pelvic girdles of pinnipeds and *Ichthyostega* are both relatively narrow and skid-like. The sacrum consists of a single, short stout rib abutting a posteriorly reinforced, anteriorly directed facet on the inner face of the ilium. Although the sacral rib of *Ichthyostega* is unknown, the large sacral facet is similarly directed and reinforced, unlike other early tetrapods in which the sacral facet is barely identifiable (e.g. *Archeria*; ROMER, 1957; *Eoherpeton*; SMITHSON, 1985). Finally, pinniped ribs also have elongate, prominent uncinate flanges, which are largest nearest to the dorsal blade of the pectoral girdle. Figure 1C shows a revised reconstruction of *Ichthyostega*, in which the posture has been altered to reflect the seal-like features of the postcranial skeleton.

Although we can only present a provisional skeletal reconstruction of *Acanthostega*, (Fig. 1A) it seems likely that it will eventually be known in considerably greater detail than our current knowledge of *Ichthyostega*. The linear dimensions of the majority of *Acanthostega* specimens are only two thirds those of most *Ichthyostega* specimens. As CLACK & COATES (this vol.) have stated, *Acanthostega* has an apparently functional gill skeleton, and a more fish-like pectoral girdle. The pelvic girdle is now known to have distinct anterior and posterior iliac processes (*contra* CLACK, 1988). Although the pelvic plate is relatively large, no clear sacral facet is present, and no sacral rib has been identified. Thus, although the nature of the sacrum remains obscure, it is clearly very different from that of *Ichthyostega*. The hind limb is already known in sufficient detail (COATES, 1991) to compare it with the hind paddle of *Ichthyostega*. The femur is more slender and elongate, but the tibia and fibula are flattened and broad, like those of *Ichthyostega*. The hind limb of *Acanthostega* is certainly longer than the fore limb, and more oar- than paddle-like. The pes is restored provisionally to have eight digits, and an ankle consisting of relatively few large components. The unusual fore limb morphology of *Acanthostega* has been discussed elsewhere (COATES & CLACK, 1990; COATES, 1991). It is remarkably fish-like, and appears to be unsuited for terrestrial use. Fore limb movement may have been restricted to a moderate degree of anterodorsal extension, and posteroventral flexion. The strap-shaped caput humeri provides a hinge-like rather than rotary joint, but this is common among early tetrapods, and apparently similar to that of *Panderichthys* (VOROBYEVA & SCHULTZE, 1991). The axial skeleton of *Acanthostega* appears to be less suited for terrestrial conditions than that of *Ichthyostega*. Each of the strongly rhachitomous vertebrae bears minimal zygapophyses and weakly ossified neural arches. The notochordal canal is unconstricted, and together with the presence of short, straight ribs (the post-pectoral distribution of which is uncertain), these features support an aquatic functional interpretation. Only the apparently xenarthrous interarticulation of mid-trunk neural arches suggests a degree of reinforcement, which may be associated with increased axial loading. The tail is already known to have longer lepidotrichia than *Ichthyostega*. Finally, the skull appears to have been more firmly bound to the pectoral girdle, *via* the anocleithra and tabular horns. Although uninformative about the degree of terrestrialisation, the presence of numerous, small conical teeth in both jaws provides a further, prominent contrast with *Ichthyostega*, which has an upper marginal dental arcade of more substantial and well differentiated teeth.

Our knowledge of *Tulerpeton* is frustratingly incomplete. LEBEDEV's (1984; 1985; 1990a) descriptions of the material show it to contain at least one form of early tetrapod that resembles

Carboniferous tetrapods more than either *Ichthyostega* or *Acanthostega*. Currently, LEBEDEV & COATES are redescribing the well articulated postcranial remains (which constitute the type material of *Tulerpeton*), and initial comparisons support this interpretation. The hexadactyl fore and hind limbs appear to be more terrestrially adapted, and although the pectoral girdle retains an anocleithrum, it lacks a post branchial lamina and no hyobranchial apparatus has been identified. The axial skeleton is known from partially preserved intercentra, but the arches, ribs, and entire tail region are missing.

The diverse morphologies of these three Late Devonian tetrapods imply an earlier evolutionary radiation, as yet only hinted at by the fragmentary remains from Australia, Scotland, and Latvia. Although SHEAR's (1991) review outlines the structure and composition of well established terrestrial ecosystems by the end of the Devonian, none of the known tetrapods appears to be terrestrial. Details of the palaeoenvironmental contexts of each of the three genera are patchy, despite the Anglo-Danish expedition of 1987 collecting valuable sedimentological data *in situ* (BENDIX-ALMGREEN *et al.*, 1990) and LEBEDEV's (1990b) review of the faunal context of *Tulerpeton*. Although a few acanthostegid specimens have been found within the *Ichthyostega* bearing sediments, the reciprocal arrangement is not known to occur. FRIEND *et al.*'s (1983) comprehensive analysis of the Devonian formations of East Greenland suggests that the fine red sandstone matrix of the *Ichthyostega* specimens corresponds to the classic palaeoenvironmental settings proposed by BARREL and ROMER. However, it has now been suggested that rather than being the product of shallow ephemeral river systems draining into a flash-flooded continental, intramontane basin (consistent with the "seasonally arid" hypothesis), the sediments may derive from tidal flats (BRAY, 1985) Reconciliation of this interpretation with the more usual placing of the East Greenland Basin within the interior of the Old Red Sandstone continent (Laurentia) (e.g. DINELEY, 1979), is achieved by the presence of a major wrench faulting system, argued to have introduced marine conditions into the Laurentian continental interior.

Most specimens of *Acanthostega* occur in contemporaneous sediments consisting of silty sandstones, fluvial channel sandstones, and overbank siltstones (BENDIX-ALMGREEN *et al.*, 1990). Sedimentological analysis indicates that *Acanthostega* was preserved in the active regions of a meandering fluvial channel system. Poorly preserved, large (50 mm diameter) lycopod branches indicate the existence of abundant vegetation within the vicinity of the channels. Invertebrate fossils are almost entirely absent from the East Greenland Devonian tetrapod deposits, represented only by burrows and arthropod trackways. The palaeoclimate is thought to have been monsoonal. The high quality of the acanthostegid fossils suggests that they were not transported far, *post-mortem*. Therefore the exclusive occurrence of *Acanthostega* within active channel deposits, and known details of the skeletal anatomy, suggest very strongly that this animal was principally aquatic; seemingly less terrestrial and more fish-like than *Ichthyostega*.

Tulerpeton, despite its closer resemblance to more recent tetrapods (and thereby assumed greater terrestriality), is found in a large, shallow marine basin, some considerable distance from the nearest known land mass. The fauna and flora are known in greater detail than either of the East Greenland deposits. LEBEDEV (1984, 1985, 1990a, b), reports the discovery of large osteolepids, dipnoans, onychodonts, holocephalans, placoderms, numerous invertebrates, charophytic algae, and stromatolites.

None of these early tetrapod environments corresponds to the seasonally arid model proposed by ROMER. Furthermore, if *Acanthostega*, *Ichthyostega*, and *Tulerpeton* are ranked according to their apparent degree of terrestriality, the result is related inversely to the supposed proximity of their remains to dry land. The thesis that ecophysiological constraints demand a freshwater tetrapod origin and emergence onto land (LITTLE, 1990), although unrefuted, is inconsistent with the most recent palaeontological data, which appears to support THOMSON's (1980) suspicion that early tetrapods lurked in brackish or saline lagoons. *Ichthyostega*'s burden as the tetrapod ancestor (as noted by MILNER *et al.*, 1986) has now been removed from its substantial shoulders. We have the prospect of at least three habitats in which to speculate about early tetrapod evolution, each of which is principally aquatic. These corroborate the proposals of GUNTER, EDWARDS, and ourselves, that limbs originated for use in water. And if the tetrapods originated and diversified in aquatic habitats, then it may be naive to prolong the debate over which particular intermediate environment provided the unique transitional route to terrestriality. Factors influencing the emersion of extant amphibious fish are now known to be extremely varied. SAYER & DAVENPORT (1991) list the following categories: environmental degradation (including oxygen concentrations, temperature, waterborne pollutants, salinity, and pH or pCO_2), biotic (including competition, predation, terrestrial feeding, and reproduction), habitat drying (apparently never investigated seriously), and voluntary emersion. We believe that it is significant that none of the 59 amphibious actinopterygian species, representing 16 marine and freshwater families, included in SAYER & DAVENPORT's review have evolved analogues of the tetrapod limb. Only in the callichthyid armoured catfishes (not even considered in SAYER & DAVENPORT's review) are stilt-like spines developed from the pectoral fins. There is clearly a need for a new, and more comprehensive examination of the terrestrialisation of tetrapods than the confines of the current manuscript will allow.

MORPHOLOGICAL TRANSFORMATION SCENARIOS

Most early attempts to formulate morphological transformation scenarios concentrated upon the change from paired fins to limbs. Key contributions to this research are summarised in SHUBIN & ALBERCH (1986). In many respects morphological scenarios require an understanding of developmental processes and patterning mechanisms, which are most effectively investigated in the domain of developmental biology. However, the description of actual rather than hypothetical transitional morphologies may provide a test of certain developmental scenarios (e.g. COATES & CLACK, 1990). And a more general, comparative method utilising the terminology of heterochrony is enabling more precise descriptions to be made of the phenotypic changes throughout phylogeny, which must result, in part, from changes in the regulation of these developmental processes.

LONG (1990a, b) has produced the most recent morphological transformation scenario to bridge the fish-tetrapod transition. The transformation passes from osteolepids, as exemplified by *Eusthenopteron foordi*, to early tetrapods, as exemplified by *Crassigyrinus scoticus*. *Acanthostega* and *Ichthyostega* are considered to be more derived than *Crassigyrinus* (because of absence of the intertemporal), and panderichthyids are referred to only sparingly. Once again,

recently published data concerning the East Greenland tetrapods and panderichthyids can provide some intriguing new perspectives on this key event in tetrapod evolution. LONG considered the role of heterochronic changes between fish and tetrapod morphologies. Paedomorphosis was suggested to have had a significant effect on the transition, with early tetrapod and small (juvenile) eusthenopterid skulls sharing many features, whereas peramorphic processes were inferred to have contributed to the transition from fin to limb. In this respect LONG's brief reviews suggested that the origin of tetrapods incorporates "dissociated heterochrony" (MCKINNEY & MCNAMARA, 1991).

LONG's assumptions concerning the condition of the skull in juvenile specimens of *Eusthenopteron* are derived from SCHULTZE's (1984) analysis of the differences between small and large individuals from the Escuminac Formation, Canada. However, SCHULTZE is careful to describe his material as a static sequence of small to large specimens, rather than as a dynamic growth series. The morphological changes, from the small (juvenile) morph in figure 2A to the large (adult) morph in figure 2B, are characterized by performing a Cartesian transformation (THOMPSON, 1942). Because of the conjecture that early tetrapod skulls are paedomorphic relative to osteolepid skulls, the skull of *Acanthostega* was subjected to the same Cartesian transformation: undistorted in figure 2D, and transformed in figure 2E, into a hypothetical adult osteolepid-like morphology. The resultant image is very similar to the lateral view of a panderichthyid skull (Fig. 2F, after VOROBYEVA & SCHULTZE, 1991). There are several ways in which this result can be interpreted. If it is assumed that (i) panderichthyids are the closest known sister-group of tetrapods, (ii) that *Acanthostega* represents the plesiomorphic tetrapod condition, and (iii) that allometric changes in eusthenopterid skull-ontogeny are conserved in early tetrapods (even if unexpressed), then the hypothesis (iv) that early tetrapod skulls are paedomorphic with respect to osteolepiforms is corroborated. The stacked assumptions underlying this conclusion indicate its extremely tenuous nature. The biological meaning of the structural transformation depicted in figure 2 is unclear. No well corroborated phylogenetic hypothesis placing panderichthyids as the sister-group of *Acanthostega* has yet been published. And if the subject of figure 2D is moved anteriorly by only 10% of the orbital width, then the result in figure 2E resembles the skull of a shovel-nosed sturgeon. Nevertheless, we regard the result of the exercise as intriguing.

Long listed a series of characters in which "juvenile" (*i.e.* small) skulls of *Eusthenopteron* resemble early tetrapods (*i.e. Crassigyrinus*). The first describes the tetrapod-like deep postorbital contribution to the orbital rim. The same pattern is exhibited in *Acanthostega*; the Cartesian transformation restricts this region similarly in the hypothetical peramorphic form, with attendant posterior expansion of the postfrontal. The second describes a notched insertion in the squamosal for the anterodorsal corner of the preopercular. This feature is absent from the panderichthyid-acanthostegid transformation. The third describes a posteriorly directed margin of the squamosal, which contributes to the opercular hinge in small eusthenopterids. This is similarly present in *Acanthostega*, where, on the basis of our description of a fish-like internal gill skeleton (COATES & CLACK, 1991), we would expect it to contribute to the support of a soft operculum. The fourth describes the extensive contribution of the jugal to the orbital rim. This is also found in *Acanthostega*. The fifth compares the presence of apparently fewer ossifications in the snout of small eusthenopterid skulls with the limited number of bones in the snout of *Crassigyrinus*; again, this character is shared with all early tetrapods. The sixth describes the shorter contact

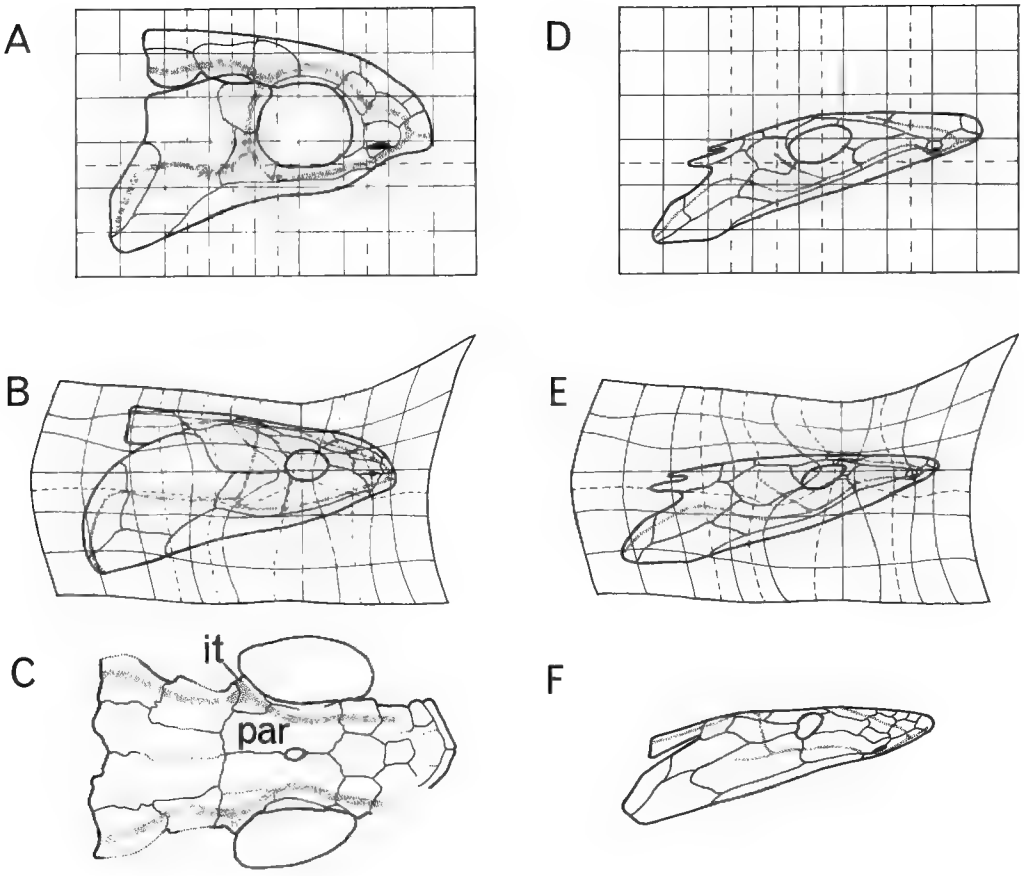

FIG. 2. — Small, large, and transformed skulls of *Eusthenopteron*, *Acanthostega* and *Panderichthys*.

A-B, Cartesian transformation of the lateral side of the skull of a small *Eusthenopteron foordi* (A), demonstrating changes towards an adult condition (B), adapted from SCHULTZE (1984, Fig. 5; mandibular, extrascapular, and operculogular bones omitted). C, skull roof of a small *Eusthenopteron foordi* in dorsal view (from SCHULTZE, 1984, Fig. 6A).

D-E, Cartesian transformation from figures A-B applied to the lateral side of the skull of *Acanthostega gunnari*. D, resulting in hypothetical peramorphic condition in figures E and F. F, side view of the skull of *Panderichthys rhombolepis* (adapted from VOROBYEVA & SCHULTZE, 1991, Fig. 37; mandibular, extrascapular, and operculogular bones omitted).

Abbr.: par, parietal; it, intertemporal.

*Petits et grands crânes transformés d'*Eusthenopteron, Acanthostega *et* Panderichthys.

A-B, transformation cartésienne d'un côté droit du crâne d'un jeune Eusthenopteron foordi *en A, montrant les changements vers la condition d'adulte en B, les plaques mandibulaires, extrascapulaires et operculogulaires ne sont pas représentées d'après* SCHULTZE *(1984, Fig. 5). C, toit crânien d'un jeune* Eusthenopteron foordi *en vue dorsale, d'après* SCHULTZE *(1984, Fig. 6A).*

*D-E, transformation cartésienne des figures A et B appliquées au côté droit du crâne d'*Acanthostega gunnari. *D, résultant de la condition péramorphique hypothétique des figures E et F. F, vue latérale du crâne de* Panderichthys rhombolepis *d'après* VOROBYEVA & SCHULTZE *(1991, Fig. 37), les plaques mandibulaires, extrascapulaires et operculogulaires ne sont pas représentées.*

Abrév. : par, pariétal ; it, intertemporal.

between the cheek unit and the skull table. Again, this change is exhibited by the acanthostegid Cartesian transformation. The convex posterior edge of the grid indicates that this is a positive allometric change; not an illusion created by the negatively allometric size of the orbit. The seventh shared feature, intricate sutures, is, as LONG notes, shared by all taxa within the present discussion, excluding adult eusthenopterids.

From the list above, only the presence of a notched squamosal supports the contention that *Crassigyrinus* represents the most primitive known tetrapod skull. Other factors used to support the peculiarly primitive interpretation of *Crassigyrinus* include the presence of an intertemporal, and SCHULTZE & ARSENAULT's (1985) observation that the dorsal position of the naris resembles the non-panderichthyid osteolepiform condition. However, the notched squamosal is regarded as convergent in the light of panderichthyid morphology. The dorsal position of the naris in *Crassigyrinus* may, alternatively, be interpreted as derived for early tetrapods, in contrast to the ventral, jaw-margin position of the naris in small eusthenopterids, panderichthyids, *Acanthostega*, *Ichthyostega*, and *Proterogyrinus* (HOLMES, 1984). Intriguingly, a primitively low position for the tetrapod naris would support WESTOLL's (1943) supposition that the dorsal migration of the naris from the jaw margin during tetrapod ontogeny (illustrated by 8-, 10-, and 15-mm human embryos) recapitulates phylogeny. The absence of an intertemporal may also derive from a paedomorphic event in near-tetrapod phylogeny. SCHULTZE's figure of a small eusthenopterid skull table (Fig. 2C) suggests that it may lack a clearly differentiated intertemporal, with the resultant parietal resembling that of *Elpistostege*, in which a lateral process occupies the intertemporal region. GODFREY (1989) describes small skulls of the colosteid *Greererpeton* which also lack intertemporals, although they are present in larger specimens. As illustrated in CARROLL's (1990) discussion of the remarkably small microsaur *Quasicaecilia*, small size appears to exert significant constraints on the osteological complexity of the tetrapod skull, and may result in total loss of the temporal series. MILNER (1988) argues that progenesis (*sensu* GOULD, 1977) has had a profound influence upon the evolution of living amphibians. We suggest that the absence of an intertemporal in *Acanthostega*, *Ichthyostega* and *Elpistostege*, may be plesiomorphic with respect to tetrapods. This may derive from a (progenetic) condition like that of the small eusthenopterid skull table, but it should be emphasised that we have no knowledge of panderichthyid ontogeny. The subsequent appearence of a tetrapod intertemporal-like bone, containing none of the sensory canals found in osteolepid intertemporals, may therefore be derived independently.

CONCLUSION

ROMER's gap between the origin and terrestrialisation of tetrapods still represents a significant void in our understanding of tetrapod evolution (at the time of writing, this gap encompasses the entire span of the Tournasian). The earliest *terrestrial* tetrapods are now known from the Visean, whereas the Late Devonian East Greenland and Russian specimens, predated by an assortment of trackways and skeletal fragments, represent a stage by which tetrapods were already morphologically diverse and occupied a range of different, but apparently aquatic, habitats. Of the three known in anatomical detail, one, *Acanthostega*, cannot be described as "already quite modern" (SHEAR, 1991), a second, *Ichthyostega*, is being revealed as increasingly unusual and

specialized in its own right, and the sedimentary and faunal context of the third, *Tulerpeton*, provides support for THOMSON's doubts about the accepted freshwater origin of tetrapods. The "Frasnian-Famennian" extinction (MCGHEE, 1989) may be a key-event in the evolution of tetrapods, which has, so far, remained unintegrated with any of the tetrapod-origin scenarios. A devastating decline in marine biodiversity appears to have been caused by a lethal temperature drop, which, in turn, triggered widespread anoxia in marine surface waters. All known early tetrapod skeletal remains coincide with, or occur after the Late Devonian mass extinction event. Evidence of widespread marine anoxia answers the principal ecophysiological objection to a non-freshwater tetrapod origin, that it is difficult to see what the selection pressures for air breathing might have been in marine conditions. Morphological data supports the hypothesis that several aspects of early tetrapod anatomy were more fish-like than had been previously supposed. As the anatomical gap between fish and tetrapod becomes narrower, the gap between origin and terrestriality becomes more clearly defined and much wider. We can begin to quantify the nature and sequence of anatomical changes more precisely. Evidence from the earliest known limb skeletons already suggests a morphologically less restrictively defined period in tetrapod evolution. Preliminary investigations into the role of heterochrony in the transition suggest a paedomorphic origin for the tetrapod dermal skull, dissociated from peramorphic evolution of the appendicular and axial endoskeleton. However, despite increased knowledge of ever closer osteolepiform relatives (the panderichthyids), we cannot yet identify the nodal location of these metamorphic events with any precision in tetrapod phylogenetic history.

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Problems of the phylogenetic analysis of paleozoic choanates

by Robert L. CARROLL

Abstract. — Phylogenetic analysis of Paleozoic tetrapods, using *Panderichthys* and *Eusthenopteron* as successive outgroups, shows *Ichthyostega, Acanthostega, Crassigyrinus*, and loxommatids as a series of outgroups of the remaining choanates. Temnospondyls plus colosteids are the sister-group of anthracosaurs and all subsequent tetrapod groups. Seymouriamorphs are the sister-group of an assemblage including two clades: one consisting of *Westlothiana*, diadectomorphs and amniotes, and the other consisting of the lepospondyl orders. Four equally parsimonious cladograms were found, two in which loxommatids were the sister-group of colosteids and temnospondyls, and two in which the position of nectrideans and microsaurs were reversed. Majority rule consensus trees up to 5 steps beyond the most parsimonious tree retained this general pattern. Because of the great amount of missing data, the actual relationships of Paleozoic tetrapods may be very different than the pattern suggested by this phylogenetic analysis. The most serious gap in our knowledge is caused by the absence of any fossil evidence of the plesiomorphic sister-groups of the major tetrapod lineages during approximately 30 million years of the Upper Devonian and Lower Carboniferous.

Keywords. — Paleozoic tetrapods, temnospondyls, colosteids, anthracosaurs, seymouriamorphs, diadectomorphs, amniotes, microsaurs, parsimony analysis, Upper Devonian, Lower Carboniferous.

Les problèmes de l'analyse phylogénétique des choanates du Paléozoïque

Résumé. — Une analyse phylogénétique des tétrapodes paléozoïques, utilisant *Panderichthys* et *Eusthenopteron* comme extragroupes successifs, montre qu'*Ichthyostega, Acanthostega, Crassigyrinus* et les loxommatides sont une série de groupes-frères pour le restant des choanates. Les temnospondyles et les colostéides regroupés en un seul ensemble constituent le groupe-frère des anthracosaures et de tous les autres tétrapodes. Les seymouriamorphes sont le groupe-frère d'un ensemble réunissant et incluant deux clades : l'un regroupe *Westlothiana*, les diadectomorphes et les amniotes : l'autre les lépospondyles. Quatre cladogrammes également parcimonieux ont été trouvés, deux dans lesquels les loxommatides sont le groupe-frère des colostéides et des temnospondyles, et deux autres où la position des nectridiens et des microsaures s'interchange. Une analyse consensuelle fondée sur la règle de la majorité maintient ce schéma général même en considérant jusqu'à cinq pas évolutifs au-delà de la topologie la plus parcimonieuse. En raison du nombre important de données manquantes, les relations entre les tétrapodes paléozoïques pourraient bien différer du schéma suggéré par cette analyse de caractères. La lacune la plus sérieuse dans nos connaissances est due à l'absence de toute donnée fossile sur les groupes-frères plésiomorphes des principales lignées de tétrapodes durant une période d'environ 30 millions d'années se situant du Dévonien supérieur au Carbonifère inférieur.

Mots-clés. — Tétrapodes paléozoïques, temnospondyles, colostéides, anthracosaures, seymouriamorphes, diadectomorphes, amniotes, microsaures, analyse de parcimonie, Dévonien supérieur, Carbonifère inférieur.

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INTRODUCTION

The fauna at Miguasha is rich and varied, with taxa representing much of the range of vertebrate diversity in the Upper Devonian. Yet, I think of this locality almost entirely in terms of the genus *Eusthenopteron* which, in many minds, epitomizes the concept of the ancestry of land vertebrates. This genus was first recognized in the 19th century, but knowledge of its anat-

omy continues to be extended (JARVIK, 1980; HITCHCOCK, 1995). *Eusthenopteron* remains the single most important genus for establishing the polarity of skeletal trait transformations throughout Paleozoic tetrapods.

All living terrestrial vertebrates can be grouped in two major assemblages – the amniotes, including reptiles, birds, and mammals, and the amphibians, including frogs, salamanders, and caecilians. Amniotes are clearly a monophyletic group, characterized by unique shared derived characters of their reproductive pattern. Unlike any other vertebrates, they possess extra-embryonic membranes – the amnion, chorion and allantois – that provide support, protection, and water retention so that the egg can be laid on land or retained in the body of the mother. Development is direct, without an aquatic larval stage. In contrast, amphibians are primitive in the absence of extra-embryonic membranes, and most genera lay their eggs in the water, as do fish, and many have an aquatic larval stage.

The ancestry of the modern amniote groups can be traced to the Upper Carboniferous where they are represented by primitive members of the mammalian clade (the Synapsida; REISZ, 1972), early diapsids (REISZ, 1981) (whose descendants include lepidosaurs, archosaurs, and birds), and the more primitive anapsids, which presumably included the ancestors of turtles (REISZ & LAURIN, 1991). These early amniotes can be recognized by a number of skeletal synapomorphies (CARROLL, 1991; SMITHSON *et al.*, 1993) that clearly differentiate them from other Paleozoic tetrapods.

In contrast, the modern amphibian orders can be traced no earlier than the Jurassic. Frogs (ESTES & REIG, 1973) and caecilians (JENKINS & WALSH, 1993) are known from the Lower Jurassic and salamanders appear in the Middle Jurassic (IVACHNENKO, 1978; ESTES, 1981). Although it is frequently assumed that the three modern amphibian groups share a unique common ancestry (MILNER, 1988; BOLT, 1991), no fossils are known that illustrate a morphology that would be expected in an immediate common ancestor, and only the frogs are generally recognized as being linked with a particular group of Paleozoic tetrapods *via* intermediate forms (RAGE & ROCEK, 1989).

The recent description of a Lower Jurassic caecilian by JENKINS & WALSH (1993) demonstrates the highly distinctive nature of this group early in its history. The retention of a primitively closed skull roof strongly suggests an origin from Paleozoic amphibians distinct from that of the open-roofed salamanders and frogs. The origin and specific relationships among the three living amphibian groups remain one of the largest scale problems in vertebrate phylogeny. Although the three major amniote groups can be traced back to the Upper Carboniferous, the affinities of ancestral amniotes with other Paleozoic tetrapods are still subject to controversy. This problem was recently exemplified in a paper by PANCHEN & SMITHSON (1988) in which alternative sister-group relationships with either anthracosaurs or microsaurs were debated.

The problems of the origin and interrelationships of the modern amphibian lineages and the specific affinities of early amniotes can only be solved by a thorough understanding of the anatomy and relationships of all groups of Paleozoic tetrapods. At present, there is no generally agreed upon phylogeny of this assemblage. Most of the groups that dominated the Upper Carboniferous and Permian are very clearly distinguished from one another when they first appear in the fossil record in the late Lower Carboniferous (CARROLL, 1992). No intermediates or plausible common ancestors are recognized. Extremely imporant studies of Devonian amphibians

by CLACK (1988, 1989, 1991, 1992), COATES & CLACK (1990, 1991, 1995), CLACK & COATES (1995), and LEBEDEV & COATES (1993) show that these genera are both much more primitive than the Carboniferous forms, and in many ways divergent. As yet, they provide little evidence as to the probable interrelationships of any later tetrapods. Skeletal remains of Upper Devonian tetrapods, and even older foot prints (THOMSON, 1993) point to the great antiquity of the group, and the extremely long gap in time between the origin of land vertebrates and the appearance of the divergent lineages in the mid-Carboniferous.

DONOGHUE *et al.* (1989) and HUELSENBECK (1991) have emphasized difficulties that may occur in establishing reliable phylogenies if the data is limited to modern taxa, without evidence of more plesiomorphic fossil relatives. In the case of Carboniferous tetrapods, all evidence comes from fossils, but the gap between the first appearance of the advanced groups in the Visean and later and the probably time of their initial divergence in the Frasnian or Famennian results in a comparable problem, since we are ignorant of the plesiomorphic sister-groups of all the derived lineages under consideration. A period of up to 50 million years may have elapsed between the time that these lineages began to differentiate in the Late Devonian, and their first appearance in the fossil record.

Fossil have been reported, but not yet described from the base of the Tournaisian (CARROLL *et al.*, 1972), but the remains are limited to a few limb bones and a neural arch. They demonstrate the presence of large labyrinthodonts, but provide little evidence of specific affinities with later groups. The oldest described Carboniferous amphibian is the limbless aïstopod *Lethiscus* from the Holkerian. New localities have been reported from the Asbian (SCHULTZE & BOLT, 1994; BOLT, 1990). The first diverse fauna is from the Brigantian of Scotland (ROLFE, 1993). The last major groups to appear are the nectrideans and lysorophids, both in the Melekessklian. Their ancestors may have diverged from other groups of tetrapods as much as 55 million years earlier.

Despite the long gap at the base of all major tetrapod lineages, establishing their probable interrelationships is greatly facilitated by knowledge of Devonian sarcopterygians such as *Eusthenopteron* which enable us to establish the polarity of character change throughout the later Paleozoic.

ABBREVIATIONS

A, B, C, D, G, I, J, K, L, X, Y,
Z, 1-10 dermal plates in lungfish, mostly without obviously homology to bones in choanates, *plaques dermiques des dipneustes sans homologies évidentes avec les os des choanates* ;
a angular, *angulaire;*
anocl anocleithrum, *anocleithrum;*
apr anterior palatal recess, *recessus palatin antérieur;*
at anterior tectal, *tectal antérieur;*
bb basibranchial, *basibranchial;*
bo basioccipital, *basioccipital;*
bhf foramen for buccohypophysial duct, *foramen pour le ductus buccohypohysaire;*
c centrale, *centrale;*
cb certobranchial, *certobranchial;*

ch	choana, *choanes;*
chy	ceratohyal, *cératohyal;*
d	dentary, *dentaire;*
dr	dorsal ridge, *ride dorsale;*
dt	distal tarsal, *tarsien distal;*
ect	ectopterygoid, *ectoptérygoïde;*
en	entopterygoid, *entoptérygoïde;*
enf	entepicondylar foramen, *foramen entépicondylaire;*
eo	exoccipital, *exoccipital;*
epb	epibranchial, *épibranchial;*
ept	epipterygoid, *épiptérygoïde;*
f	frontal, *frontal;*
fb	fossa Bridgei, *fosse de Bridge;*
fe	femur, *fémur;*
fib	fibula, *péronné;*
fiba	fibulare, *fibulaire;*
fm	foramen magnum, *foramen magnum;*
fp	footplate of stapes, *base du stapes;*
gp	gular plate, *plaque gulaire;*
h	humerus, *humérus;*
hh	hypohyal, *hypohyal;*
hy	hyomandibular, *hyomandibulaire;*
hyf	facet for hyomandibular, *facette pour l'hyomandibulaire;*
i	intermedium, *intermédiaire;*
in	internasal, *internasal;*
infb	infrapharyngobranchial, *infrapharyngobranchial;*
it	intertemporal, *intertemporal;*
j	jugular, *jugulaire;*
juv	jugular vein, *veine jugulaire;*
l	lacrimal, *lacrymal;*
les	lateral extrascapular, *extrascapulaire latéral;*
lptr	lateral palatal tooth row, *rangée dentaire palatale latérale;*
lr	lateral rostral, *rostral latéral;*
m	maxilla, *maxillaire;*
mes	medial extrascapula, *extrascapulaire médial;*
mr	medial rostral, *rostral médial;*
n	nasal, *nasal;*
na	external naris, *narine externe;*
nc	notochordal canal, *canal notochordal;*
nscav	nasal cavity, *cavité nasale;*
orbart	orbital artery, *artère orbitaire;*
oo	otic-occipital portion of braincase, *partie otico-occipitale du neurocrâne;*
op	operculum, *opercule;*

opis	opisthotic, *opisthotique;*
p	parietal, *pariétal;*
pal	palatine, *palatin;*
palf	palatal fang, *croc palatin;*
pdp	palatal dental plates, *plaque dentaire palatine;*
pf	postfrontal, *postfrontal;*
pm	premaxilla, *prémaxillaire;*
po	postorbital, *postorbitaire;*
pop	preopercular, *préoperculaire;*
pp	postparietal, *postpariétal;*
prf	prefrontal, *préfrontal;*
ps	parasphenoid, *parasphénoïde;*
psp	presplenial, *présplénial;*
pt	pterygoid, *ptérygoïde;*
ptf	post-temporal fossa, *fosse post-temporale;*
ptt	post-temporal, *post-temporal;*
q	quadrate, *carré;*
qj	quadratojugal, *quadratojugal;*
r	rostral, *rostral;*
ra	radius, *radius;*
re	radiale, *radial;*
rmi	ramus mandibularis internus, *rameau nerveux mandibulaire interne;*
sa	surangular, *surangulaire;*
sbm	submandibulo-branchiostegal plate, *plaque submandibulaire branchiostégale;*
sbr	sublingual rod, *tige sublinguale;*
sc-co	scapulocoracoid, *scapulocoracoïde;*
scl	supracleithrum, *supracleithrum;*
smbp	submandibulo-branchiostegal plate, *plaque submandibulaire branchiostégale;*
sop	subopercular, *sous-operculaire;*
sp	splenial, *splénial;*
spb	suprapharyngobranchial, *banchial suprapharyngien;*
spcl	spiracular cleft, *fente spiraculaire;*
sph	sphenethmoid portion of braincase, *région sphénethmoïde du neurocrâne;*
spr	spiracle, *spiracle;*
sq	squamosal, *squamosal;*
st	supratemporal, *supratemporal;*
start	stapedial artery, *artère stapédiale;*
stb	distal blade of stapes, *lame distale du stapes;*
stf	foramen for stapedial artery, *foramen pour l'artère stapédiale;*
sty	stylohyal, *stylohyal;*
t	tabular, *tabulaire;*
thy-m	truncus hyoideo-mandibularis, *tronc hyoïdo-mandibulaire;*
ti	tibia, *tibia;*

u	ulna, *ulna;*
ul	ulnare, *ulnaire;*
urh	hurohyal, *hurohyal;*
v	vomer, *vomer;*
vf	vomerine fang, *croc vomérien.*

METHODOLOGY

Several factors must be established before we can determine the interrelationships among Paleozoic tetrapods.

A – Determine that they are a monophyletic assemblage.

B – Establish the polarities of all characters that vary within the group.

C – Establish that the subgroups (the orders of Paleozoic tetrapods) are each monophyletic on the basis of unique apomorphies.

D – Determine the derived character-states present in the most primitive members of each monophyletic subgroup.

E – Determine the homology of these derived characters from group to group.

1) The first of these requirements has been met through the work of GAFFNEY (1979), PANCHEN & SMITHSON (1987), GODFREY (1989), VOROBYEVA & SCHULTZE (1991), and CLACK & COATES (1995) who have recognized many features that demonstrate the monophyly of tetrapods. More than 50 derived characters are recognized in this study, uniting tetrapods and differentiating them from choanate sarcopterygians. If, as argued by these authors, tetrapods are monophyletic, their origin from osteolepiform sarcopterygians (including panderichthyids) is a singular event that is the logical point from which to initiate phylogenetic analysis of all tetrapods.

2) The next task is to establish the most appropriate outgroup for determining the polarity of character state transformation among early tetrapods. This outgroup should be the most closely related sister-group within the larger monophyletic assemblage including the group in question.

ROSEN *et al.* (1981) may be correct in claiming that lungfish are the closest living sister-group of tetrapods, but extensive evidence has accumulated to support much closer common ancestry between Paleozoic tetrapods and Devonian osteolepiforms (including panderichthyids) ALBERG (1991), LONG (1990), PANCHEN & SMITHSON (1987), THOMSON (1993), SCHULTZE (1986), YU (1990).

VOROBYEVA & SCHULTZE (1991) listed the folowing synapomorphies as uniting osteolepiforms and tetrapods.

1. One external nasal opening.
2. Choana between premaxilla, maxilla, vomer, and dermopalatine.
3. Median rostral fused with premaxilla.
4. Few unpaired or paired postrostrals.
5. Lateral rostral ventral to external naris.
6. Large lacrimal.
7. Narrow preopercular bone at posterior margin of cheek.
8. Palatal recess unpaired and without bone cover.

9. Two-headed articulation of ribs.
10. Tetrapod articulation between humerus and scapulocoracoid.
11. Tetrapod pattern of proximal limb elements.

Much more detailed comparison can be made between Devonian osteolepiforms and tetrapods than between either of these groups and the Dipnoi. Illustrations of a representative Devonian lungfish *Chirodipterus* are included in figures 1-3 to emphasize this fact. Every major bone in the skull, vertebral column and appendicular skeleton of osteolepiformes can be directly compared with bones in the same relative position in early tetrapods. In contrast, very few skull bones in Dipnoi can be homologized with counterparts in either osteolepiforms or tetrapods. The vertebrae and limbs are also clearly distinct. It would be impossible to establish the polarity of the majority of character transformations in early tetrapods on the basis of the characters in any lungfish.

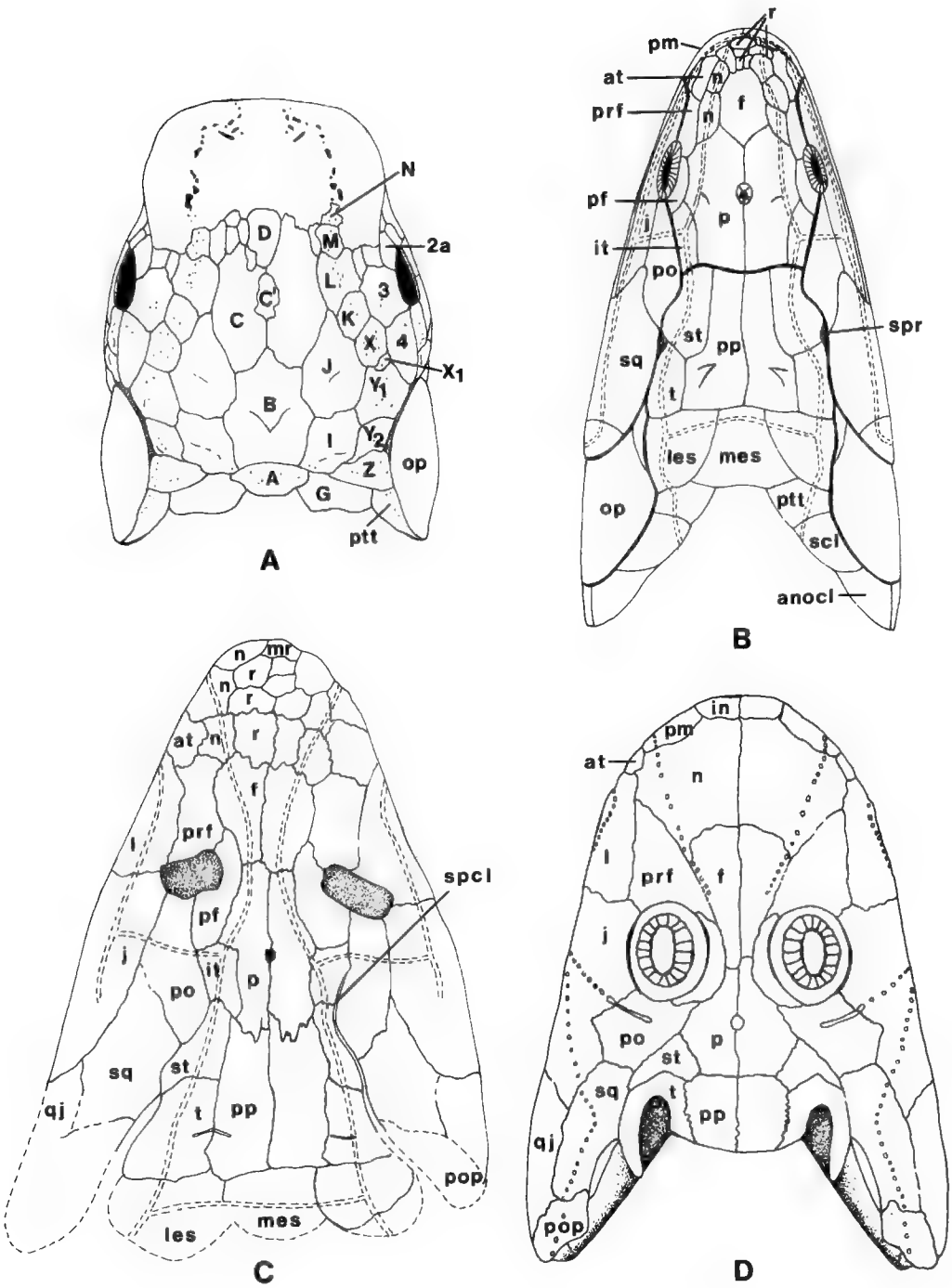
We are extremely fortunate in our work on early tetrapods to have knowledge of the osteolepiforms *Eusthenopteron* and *Panderichthys* to establish the primitive character state of most of the skeletal characters that change within the choanates. Starting with the character states that are present in these genera, we can recognize the polarity of transformations in nearly even bone in the body of early land vertebrates.

3) The monophyletic origin of most of the previously recognized groups of Paleozoic tetrapods can be demonstrated on the basis of readily recognized apomorphies.

Acanthostega: unique configuration of tabular, accessory articulation of neural arches without well-formed zygopophyses.
Ichthyostega: median postparietal, unique pattern of attachment of braincase to back of skull table.
Crassigyrinus: unique size disparity of fore and hind limb, extremely deep cheek.
Loxommatids: keyhole shaped orbits.
Anthracosaurs: long tabular horn, 5th digit of pes with five phalanges, functionally embolomerous vertebrae.
Seymouriamorphs: stapes articulating with tabular, unique pattern of swollen neural arches.
Westlothiana: amniote pattern of skull table, but 36 presacral vertebrae, forelimb much smaller than rear, but not of pattern in *Crassigyrinus*.
Diadectomorphs: solid attachment of supraoccipital with dermal bones of occiput.
Amniotes: supra-occipital a broad plate of bone, loosely attached to postparietal and tabular dorsally, small supratemporal, tabular and paired postparietal, canine teeth.
Nectrideans: haemal arches fused to middle of centrum, symmetrical to neural arches.
Aïstopods: extremely elongate body, reduction or absence of girdles, absence of limbs, first cervical centrum articulates with circular depression in occiput.
Microsaurs: skull table lacking supratemporal, tabular reaching postorbital and in some families the postfrontal.
Adelogyrinids: a single bone, bearing a posterior process, occupies the position of the tabular, supratemporal and squamosal of other early tetrapods, postorbital reduced and does not enter margin of orbit, limbs and endochondral girdles lost but dermal shoulder girdle well-developed.
Lysorophids: open cheek, jaw suspension angled forward, limbs greatly reduced.
Temnospondyls: impedance matching middle ear.
Colosteids: "canine" teeth in premaxillae, closure of squamosal embayment.

This list is short, but not contradicted by other characters.

Some of these groups may be paraphyletic. There is considerable evidence that temnospondyls are the sister-group of modern anurans, and possibly of other modern amphibians (MILNER, 1988). Microsaurs have been suggested as including the sister-taxa of caecilians (CARROLL & CURRIE, 1975; WALSH, 1987) and possibly urodeles (CARROLL & HOLMES, 1980). Diadectomorphs probably include the sister-group of amniotes (SMITHSON *et al.*, 1993).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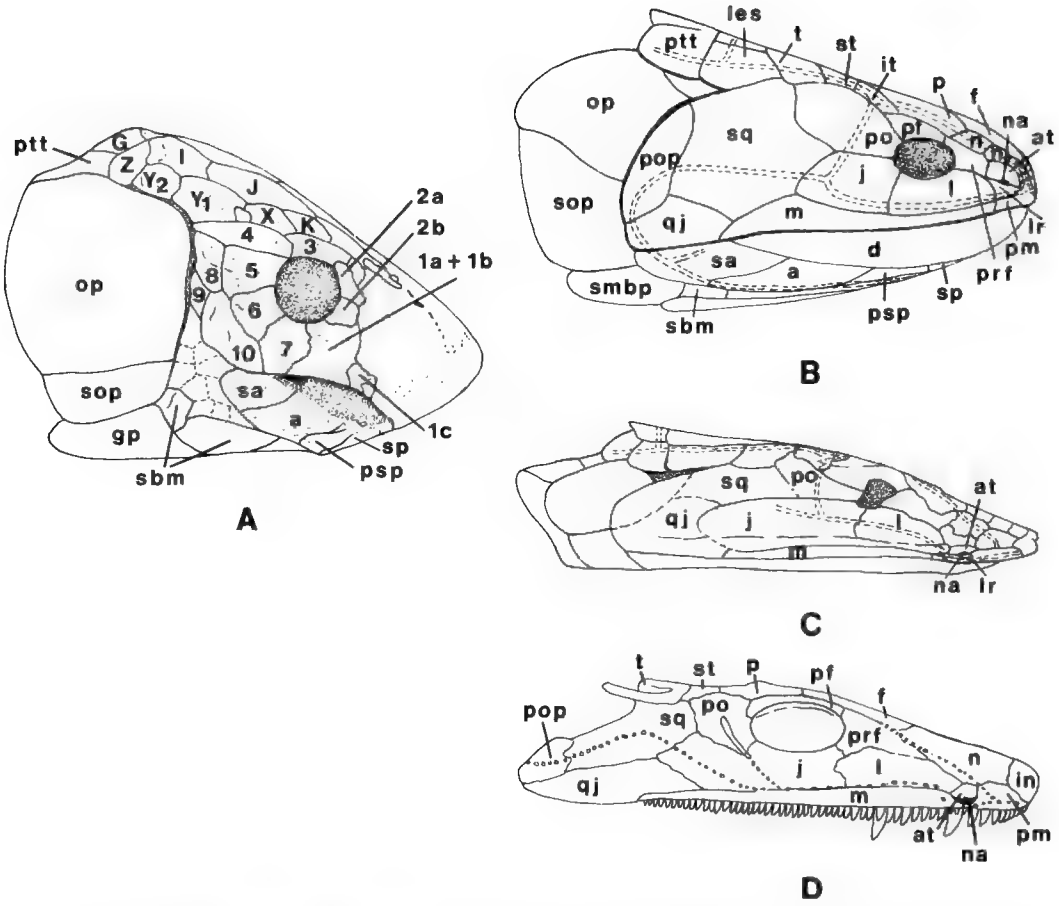
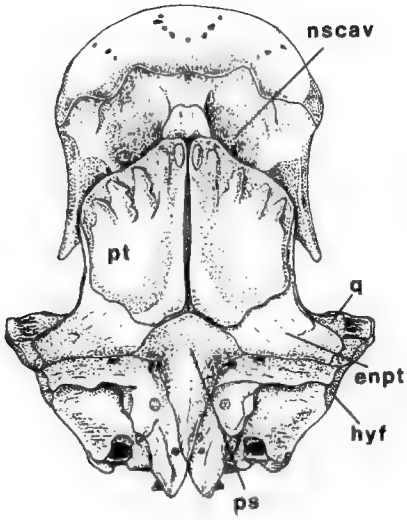


FIG. 2. — Lateral views of skull of sarcopterygians and *Acanthostega*. A, the lungfish *Chirodipterus* (modified from MILES, 1977). B-C, the osteolepiform rhipidistians *Eusthenopteron* (modified from JARVIK, 1980) and *Panderichthys* (modified from VOROBYEVA & SCHULTZE, 1991). D, *Acanthostega* (drawing supplied by Dr CLACK).

*Crânes de sarcoptérygiens et d'*Acanthostega *en vues latérales. A,* Chirodipterus, *un dipneuste (modifié d'après* MILES, *1977). B-C, crossoptérygiens rhipidistiens,* Eusthenopteron *(modifié d'après* JARVIK, *1980) et* Panderichthys *(modifié d'après* VOROBYEVA & SCHULTZE, *1991). D,* Acanthostega *(dessin Dr* CLACK*).*

FIG. 1. — Skull roof of sarcopterygians and *Acanthostega*. A, the lungfish *Chirodipterus* (modified from MILES, 1977). B-C, the osteolepiform rhipidistians *Eusthenopteron* (modified from JARVIK, 1980) and *Panderichthys* (modified from VOROBYEVA & SCHULTZE, 1991). D, *Acanthostega* (drawing supplied by Dr CLACK). Heavy lines on the skull of *Eusthenopteron* indicate the lines of mobility between the elements of the dermal skull.

*Toits crâniens de sarcoptérygiens et d'*Acanthostega. *A,* Chirodipterus, *un dipneuste (modifié d'après* MILES, *1977). B-C, crossoptérygiens rhipidistiens,* Eusthenopteron *(modifié d'après* JARVIK, *1980) et* Panderichthys *(modifié d'après* VOROBYEVA & SCHULTZE, *1991). D,* Acanthostega *(dessin Dr* CLACK*). Les traits gras sur le toit crânien d'*Eusthenopteron *indiquent les zones de mobilité entre les éléments du toit crânien dermique.*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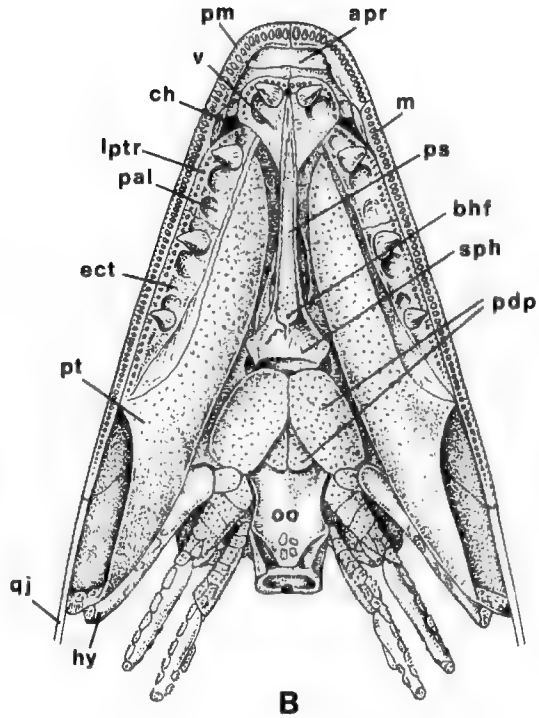
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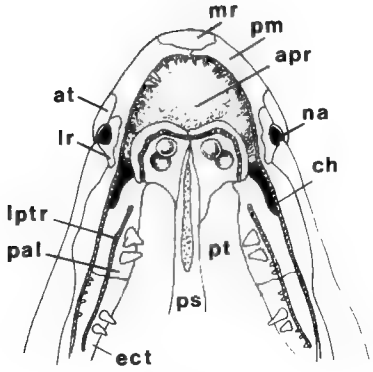
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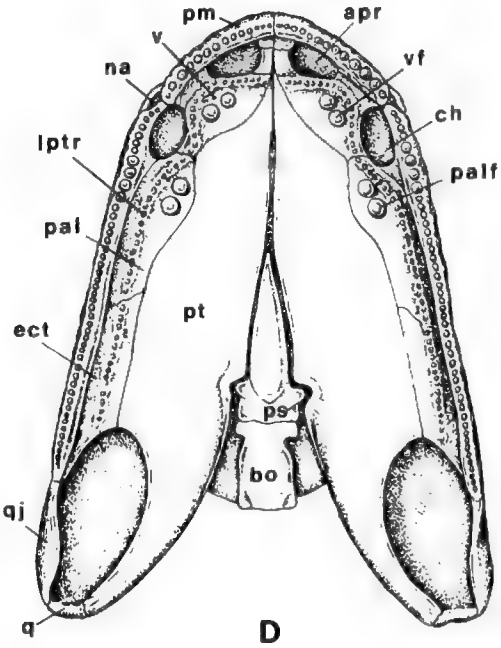
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4) It is a great deal more difficult to establish what derived characters were present in the earliest members of the various lineages. The well known fossils of all orders are characterized by many derived characters (appendix I and III), but any or all may have evolved during the 25 million years or more between the initial radiation of tetrapods, sometime in the Middle to Upper Devonian, and the appearance of more derived groups in the late Lower Carboniferous. Obviously, only those characters that were present in the earliest members of these groups can demonstrate sister-group relationships with other groups of Paleozoic tetrapods (DONOGHUE, 1989).

5) The absence of knowledge of any tetrapods during the first 25 million years of the Carboniferous also makes it extremely difficult to establish the specific homology of derived characters that are present in different lineages in the later Carboniferous. Only those characters that had evolved in the common ancestors of two or more lineages can be accepted as strictly homologous. In the absence of any immediate ancestors, it is impossible to establish directly whether or not characters in divergent lineages are homologous. On the other hand, it may be possible to establish the probability of similar derived characters being homologous on the basis of character changes within monophyletic groups. The absence of the character state in question in some members of one (or both) of the groups suggests that its presence in other members is the result of convergence.

There are certainly many examples of similar derived conditions having evolved convergently among different groups of Paleozoic tetrapods, each of which are differentiated by autapomorphies : elaboration of large interpterygoid vacuities in advanced (but not primitive) nectrideans as well as in ancestral temnospondyls; sutural attachment of the basicranial articulation in advanced, but not primitive, members of both groups; closure of the squamosal embayment in limnoscelid diadectomorphs, colosteids, some temnospondyls, and in the lepospondyl groups; fusion of the proximal tarsals into an astragalus in the ancestors of amniotes, among gephyrostegid anthracosaurs and among microsaurs; sutural attachment of cheek and skull table among advanced nectrideans, anthracosauroids (*Anthracosaurus* and seymouriamorphs), reptiles, and microsaurs; loss of the intertemporal in advanced but not primitive temnospondyls, and advanced but not primitive loxommatoids.

Convergence, or homoplasy is certainly a common feature of these groups, but even more common are characters for which there is no obvious evidence as to whether they are homologous or convergent. Spool-shaped centra occur in amniotes, lepospondyls, and lissamphibians, but we have no idea of the degree of homology of these structures (CARROLL & CHORN, 1994). Loss characters are common examples. Many groups lack the intertemporal bone (reptiles, *Ichthyostega*, *Acanthostega*, microsaurs, nectrideans) but is this absence homologous? Other examples

FIG. 3. — Palatal views of the skulls of sarcopterygians and *Acanthostega*. A, the lungfish *Chirodipterus* (modified from MILES, 1977). B-C, the osteolepiform rhipidistians *Eusthenopteron* (modified from JARVIK, 1980) and *Panderichthys* (modified from VOROBYEVA & SCHULTZE, 1991). D, *Acanthostega* (drawing supplied by Dr CLACK).

*Toits crâniens en vue palatale de sarcoptérygiens et d'*Acanthostega. *A*, Chirodipterus, *un dipneuste (modifié d'après* MILES, *1977). B-C, crossoptérygiens rhipidistiens,* Eusthenopteron *(modifié d'après* JARVIK, *1980) et* Panderichthys *(modifié d'après* VOROBYEVA & SCHULTZE, *1991). D,* Acanthostega *(dessin Dr* CLACK*).*

include reduction of toes in the manus in temnospondyls, microsaurs, and lysorophids, loss of palatal fangs in limnoscelids, amniotes, and all lepospondyl groups, and loss of limbs in adelogyrinids and aïstopods. The common practice in forming data matrices for phylogenetic analysis is to code these derived characters as if they were homologous, but this practice is not justified if there is no way of determining whether they represent one character (if they are homologous) or two or more different characters (if they are not). Unfortunately, there is no procedure in the currently available phylogenetic packages for handling this type of uncertainty. It is commonly argued that convergence is rare and that homoplasy can be established by incongruence with other character transformations once the data is analyzed, but if the number of homoplastic characters approach 50% of those being analyzed, it becomes impossible to identify them (CARROLL & CURRIE, 1991; SCOTT & JANIS, 1993).

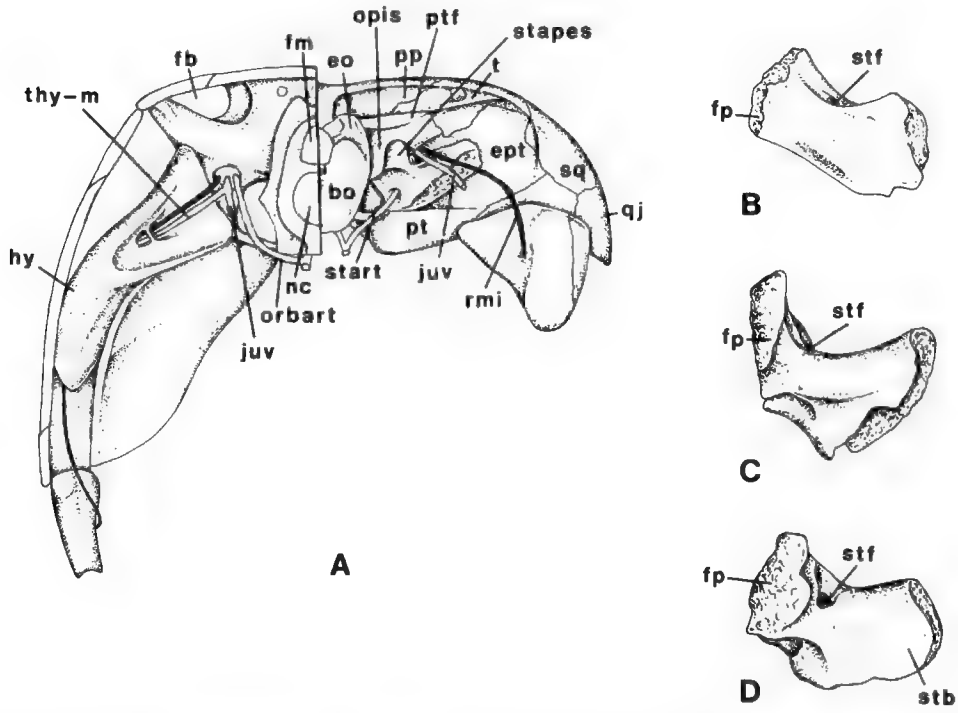


FIG. 4. — Comparison of the hyomandibular in a rhipidistian and the stapes of tetrapods. A, composite drawings of the occiputs of *Eusthenopteron* (on the left) and *Greererpeton* (on the right) showing the change in the pattern of blood vessels and nerves related to the configuration of the hyomandibular and stapes (modified from SMITHSON, 1982). B, stapes of *Acanthostega* (modified from CLACK, 1992). C, stapes of the embolomere *Pholiderpeton* (modified from CLACK, 1992). D, stapes of the temnospondyl *Greererpeton* (modified from SMITHSON, 1982).

*Comparaison entre l'hyomandibulaire d'un rhipidistien et le stapes des tétrapodes. A, dessins composites des régions occipitales d'*Eusthenopteron *(à gauche) et de* Greererpeton *(à droite) montrant le changement dans la disposition des vaisseaux sanguins et des nerfs en rapport avec la position de l'hyomandibulaire et du stapes (modifié d'après* SMITHSON, *1982). B, stapes d'*Acanthostega *(modifié d'après* CLACK, *1992). C, stapes de l'embolomère* Pholiderpeton *(modifié d'après* CLACK, *1992). D, stapes du temnospondyle* Greererpeton *(modifié d'après* SMITHSON, *1982).*

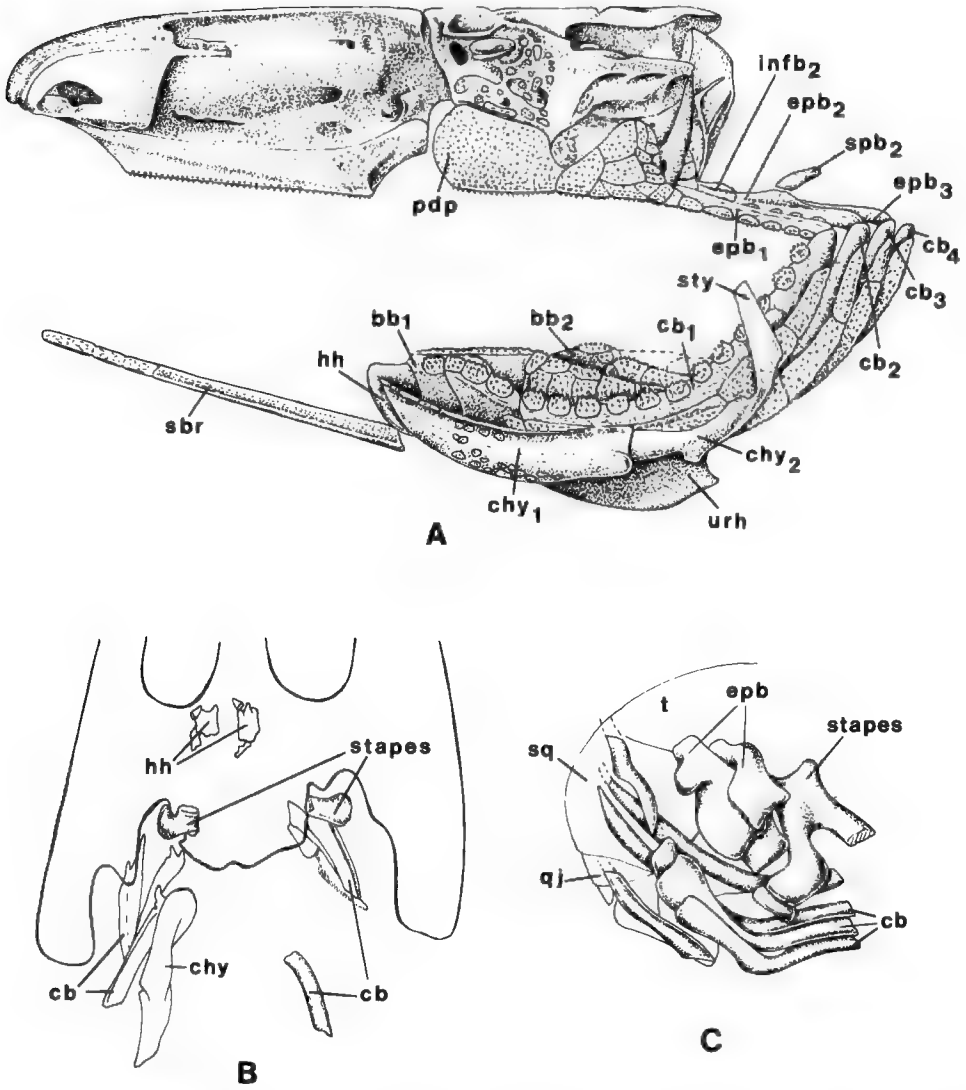


FIG. 5. — Hyoid apparatus of choanates. A, *Eusthenopteron* (modified from JARVIK, 1980). B, *Acanthostega* (modified from COATES & CLACK, 1991). C, hyoid of *Pantylus* (modified from ROMER, 1969).

Appareil hyoïdien de choanates. A, Eusthenopteron *(modifié d'après* JARVIK, *1980). B,* Acanthostega *(modifié d'après* COATES & CLACK, *1991). C, os hyoïde de* Pantylus *(modifié d'après* ROMER, *1969).*

Unfortunately, there are no immediate ways around the problems of identifying which derived characters were present in the earliest members of the monophyletic subgroups, or determining the homology of the characters that are present when the groups do appear in the fossil record. One may only hope that the derived characters of the earliest known members of

the individual groups reflect the condition in earlier members, and that most similar derived characters are homologous. These problems must be borne in mind in considering the data presented here.

TAXA AND CHARACTERS

Thanks to the exhaustive descriptive work of JARVIK (1980, and works cited therein), ANDREWS & WESTOLL (1970), and others, nearly every aspect of the skeletal anatomy of *Eusthenopteron* is known in great detail. *Panderichthys* is less completely known, but shows numerous derived characters in common with early tetrapods that indicate that it is the closest sister-taxon of any currently known genus (VOROBYEVA & SCHULTZE, 1991).

All of the major groups of Paleozoic tetrapods have been considered, along with several individual genera of particular anatomical or phylogenetic significance. One isolated genus that represents a distinct anatomical pattern, *Acherontiscus* (CARROLL, 1969b), was not included here because the cranial anatomy is very incompletely known and the large number of gaps in the data set would reduce the value of known character states in other taxa.

Data of tetrapod taxa were taken from the following sources.

Acanthostega: CLACK (1988, 1989, 1991, 1993, and in press), COATES & CLACK (1990, 1991), CLACK & COATES (1995) and pers. comm.

Ichthyostega: JARVIK (1980, and references cited therein), CLACK (1988, 1989, 1993, 1995), COATES & CLACK (1990, 1991) and pers. comm.

Crassigyrinus: PANCHEN (1985), PANCHEN & SMITHSON (1990), CLACK (1994).

Loxommatids: BEAUMONT (1977); pending redescription, *Spathicephalus* is assumed to be a member of this assemblage.

Anthracosaurs: including *Proterogyrinus* and other embolomeres HOLMES (1980, 1984), PANCHEN (1970, 1980), *Eoherpeton* SMITHSON (1985), and gephyrostegids CARROLL (1970), BOY & BANDEL (1973).

Seymouriamorphs: including Seymouriidae WHITE (1939), BERMAN *et al.* (1987), Michael LAURIN (pers. comm.) and Discosauriscidae SPINAR (1952).

Westlothiana: SMITHSON (1989), SMITHSON & ROLFE (1990), SMITHSON *et al.* (1993).

Diadectomorphs: Limnoscelidae ROMER (1946), FRACASSO (1987), Tseajaiidae MOSS (1972), Diadectidae SUMIDA & LOMBARD (1991). *Limnoscelis* was used exclusively as a basis of establishing the primitive character states of this group.

Amniotes: Pelycosaurs, protorothyrids, Carboniferous diapsids CARROLL (1964, 1969a, 1982, 1986b, 1991), REISZ (1972, 1981).

Nectrideans: BOSSY (1976), A. C. MILNER (1977), A. C. MILNER (1980).

Aïstopods: BAIRD (1964), MCGINNIS (1967), WELLSTEAD (1982), and CARROLL (work in progress).

Microsaurs: CARROLL & GASKILL (1978), CARROLL (1992), CARROLL *et al.* (1991).

Adelogyrinids: ANDREWS & CARROLL (1991).

Lysorophids: WELLSTEAD (1991).

Temnospondyls: A. R. MILNER (1990, 1993).

Colosteidae: SMITHSON (1982), GODFREY (1989), and HOOK (1983).

The most primitive character states recognized within each group were established (appendices I & II). In drawing up the character list, all aspects of the skeleton were evaluated. Beginning with *Eusthenopteron*, all characters were considered that differed significantly among these taxa. Some were not considered further because their state was not known in many taxa. Others were omitted because they showed very great variability within one or more groups and so it was difficult to establish the primitive state for each. For example the pattern of dermal sculpturing, and the specific number of marginal teeth.

Although not an exhaustive list, the characters are representative of all aspects of the skeletal system. If all these characters were known in the earliest members of all these groups, they would almost certainly be sufficient to establish their branching sequence.

COMMENTS ON SELECTED CHARACTERS

4. The general course of the lateral line canals on the skull of osteolepiforms exhibits a consistent pattern which is variously altered in different groups of tetrapods. Unfortunately this is a very difficult character to use in phylogenetic analysis. The osteolepiform pattern may be present during early development in all Paleozoic amphibians that retain a distinct aquatic larval stages. The conspicuous expression of the canals in permanently aquatic Triassic amphibians illustrates the ease with which this system can revert to a primitive pattern.

6. This is one of the few characters for which the state in the immediate tetrapod ancestor is contentious. Apparently the ventral orientation is derived among the most primitive tetrapods, and then reverses in the ancestor(s) of the advanced lineages.

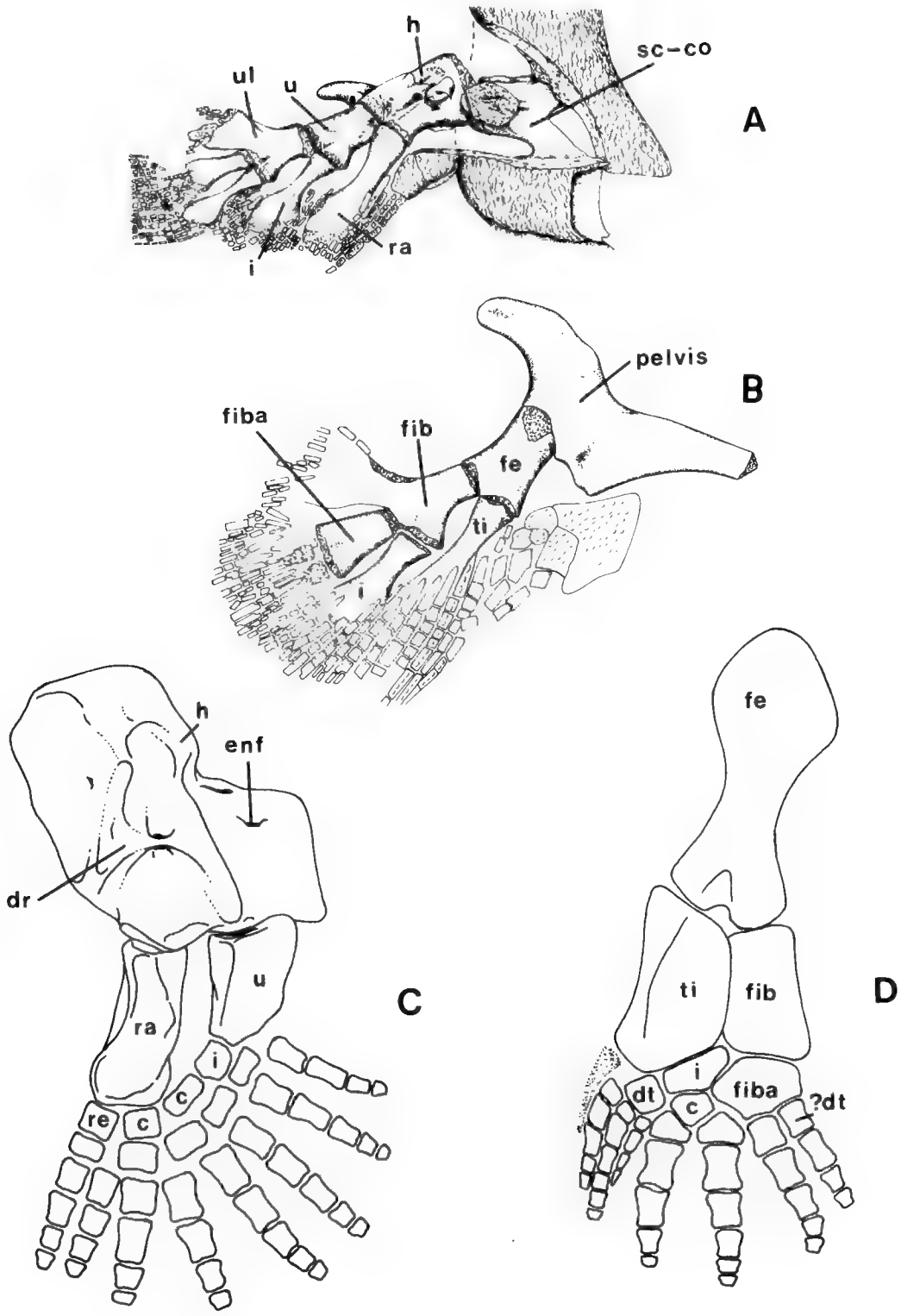
17-18. There is question regarding the homology of the tetrapod septomaxilla. PANCHEN (1967) made a strong case for homology with the lateral rostral, but CLACK (1993) pointed out positional similarity between the bone identified as the septomaxilla in loxommatids and the anterior tectal.

24. BOLT (1990) has reported the discovery of a Mississippian tetrapod exhibiting many features of later anthracosaurs but possessing the more primitive pattern of the skull roof in which the tabular is separated from the parietal by the supratemporal. Unfortunately, it is awkward to include the few character states of this animal that have so far been mentioned in the literature without being able to make comparison with the scores of other characters that can be cited for other taxa.

31. In all temnospondyls and colosteids there is an extensive open space between the palatal ramus of the pterygoid and a narrow cultriform process of the pterygoid. In other taxa, including some microsaurs and lysorophids represented only by genera with much smaller skulls, there is a large space between the palatal rami of the pterygoids, occupied by the relatively wider base of the braincase, but the remainder of the skulls are so different that there is very little likelihood that the character is homologous.

70. The medial surface of the lower jaw varies considerably in the presence or absence of large openings and the specific distribution of smaller fenestra. These differences have no obvious relationship to major phylogenetic divisions, but are included in the data set since they may eventually prove useful in characterizing taxa at some hierarchical level.

83. As in the case of the lateral line canals, the hyoid apparatus may have been highly elaborated and relatively similar in the early larval stages of most Paleozoic tetrapods. The configuration in the few adults in which it is known differ widely (Fig. 6, see also ANDREWS & CARROLL, 1991), but there is little evidence that the differences can be associated with particular taxonomic groups.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92, 102. The most striking feature by which *Panderichthys* differs from most early tetrapods and other osteolepiforms is in the absence of pleurocentra. Since this condition also exists in two groups of early tetrapods it may be an important clue to their affinities. Unfortunately there is no way to be certain of the polarity of the character change or the homology of the character states.

104. The area of the sacrum is not exposed in any of the known specimens of *Acanthostega* or *Ichthyostega*. For that reason, this character is scored as ? The presence of a well-defined iliac blade, however, strongly indicates that at least one vertebra must have served the role of a sacral.

150, 151, 152, 153, 154, 172-177. Carpals and tarsals are frequently poorly ossified and are only rarely well-articulated. Their number and pattern has the potential to be useful in phylogenetic studies, but the rarity of adequately preserved material means that these data cannot be relied on at present.

No characters have been weighted or constrained from reversal. Some characters such as the degree of torsion of the humerus and posterior extent of the parasphenoid presumably evolved progressively within particular lineages, but since comparison is being made between lineages as well, there is no evidence that change was progressive between the particular taxa in which these characters are known. Hence, no characters have been ordered.

PHYLOGENETIC ANALYSIS

The character list and data matrix are shown in appendices I and II. Illustrations of sarcopterygians and early tetrapods are shown in Figures 1-6. Other illustrations of more derived Paleozoic tetrapods appear in CARROLL (1992). The data matrix was processed by the phylogenetic package PAUP, 3.1 (SWOFFORD, 1993), run on a Macintosh LC III, using the Deltran option. The four shortest trees have 454 steps. Tree 2 appears as figure 7. *Panderichthys* and *Eusthenopteron* appear as successive outgroups of tetrapods. *Acanthostega*, *Ichthyostega*, *Crassigyrinus*, and loxommatids succeed one another as progressively more derived tetrapods. They are followed by a group consisting of colosteids and temnospondyls which appears as the sister-group of all more derived tetrapods. The next more derived group is the anthracosaurs, followed by the seymouriamorphs. The seymouriamorphs are the sister-group of all other early tetrapods, which are represented on one hand by *Westlothiana*, diadectomorphs and amniotes, and on the

FIG. 6. — Fore and hind limbs of rhipidistian and tetrapods. A-B, fore and hind limbs of *Eusthenopteron* (modified from ANDREWS & WESTOLL, 1970). C, forelimb of *Acanthostega*. Position and identification of carpals very speculative. D, hindlimb of *Ichthyostega*. (C-D, courtesy of Dr COATES).

*Membres antérieurs et postérieurs de rhipidistiens et de tétrapodes. A-B, membres antérieurs et postérieurs d'*Eusthenopteron *(modifié d après* ANDREWS & WESTOLL, *1970). C, membre antérieur d'*Acanthostega. *La position et l'identification des carpiens sont très hypothétiques. D, membre postérieur d'*Ichthyostega. *(C-D, avec l'aimable autorisation du Dr* COATES*).*

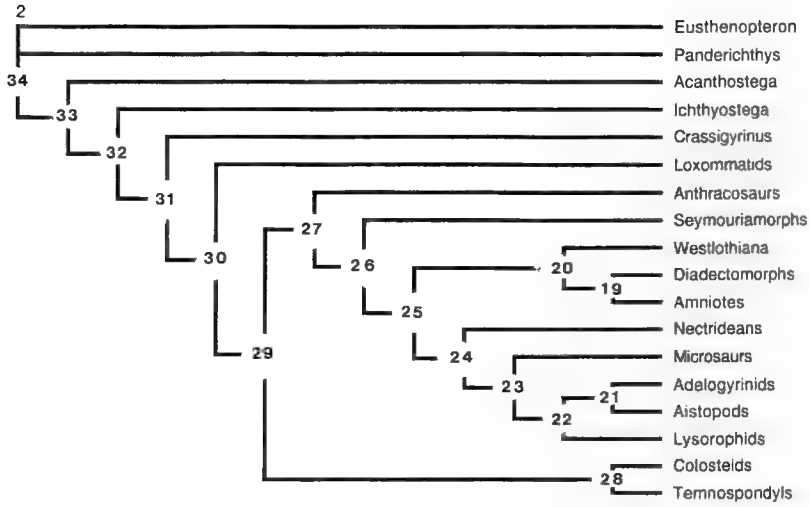


FIG. 7. — Cladogram of Paleozoic choanates. One of four most parsimonious trees generated by PAUP 3.1 using the Deltran option, based on data matrix in Appendix II. Apomorphy list reproduced as Appendix III.

Cladogramme des choanates paléozoïques. L'un des quatre arbres le plus parcimonieux généré par PAUP 3.1 en utilisant l'option Deltran, d'après la matrice de données de l'appendice II. La liste des apomorphies est donnée dans l'appendice III.

other hand by the lepospondyl assemblage. The other three most parsimonious trees (Fig. 8) differ in having loxommatids as the sister-group of colosteids and temnospondyls, or in the relative position of the microsaurs and nectrideans among the lepospondyls. These trees fit the general impression of the affinities of the "labyrinthodonts" as a sequence of progressively more derived groups, the lepospondyls as a natural group, and the amniotes allied with diadectomorphs. It is somewhat unexpected to find the seymouriamorphs as the sister-group of lepospondyls as well as amniotes.

If the number of steps is increased by one, the number of trees increases by three. In two, *Westlothiana* is the sister-group of amniotes, rather than of diadectomorphs and amniotes, and in one temnospondyls and colosteids are together more derived than the anthracosaurs.

Among the 24 trees with 456 steps, the following novelties appear : amniotes as the plesiomorphic sister-group of diadectomorphs and *Westlothiana*, loxommatids and loxommatids plus temnospondyls, and colosteids as the sister-group of seymouriamorphs and all more advanced tetrapods, nectideans rather than lysorophids as the sister-group of adelogyrinids and aïstopods, nectrideans and lysorophids as sister-taxa, *Westlothiana* as the sister-group of the lepospondyls and this assemblage as the sister-group of the diadectomorphs and amniotes, and *Westlothiana* as the sister-group of the assemblage including diadectomorphs, amniotes and lepospondyls.

Fifty-three trees were generated at 457 steps, just three more than the most parsimonious. A strict consensus of these trees resulted in a polytomy involving the common ancestors of colosteids and temnospondyls with *Crassigyrinus*, loxommatids, anthracosaurs, and the common ancestors of all more derived tetrapods. A second polytomy involves *Westlothiana*, diadecto-

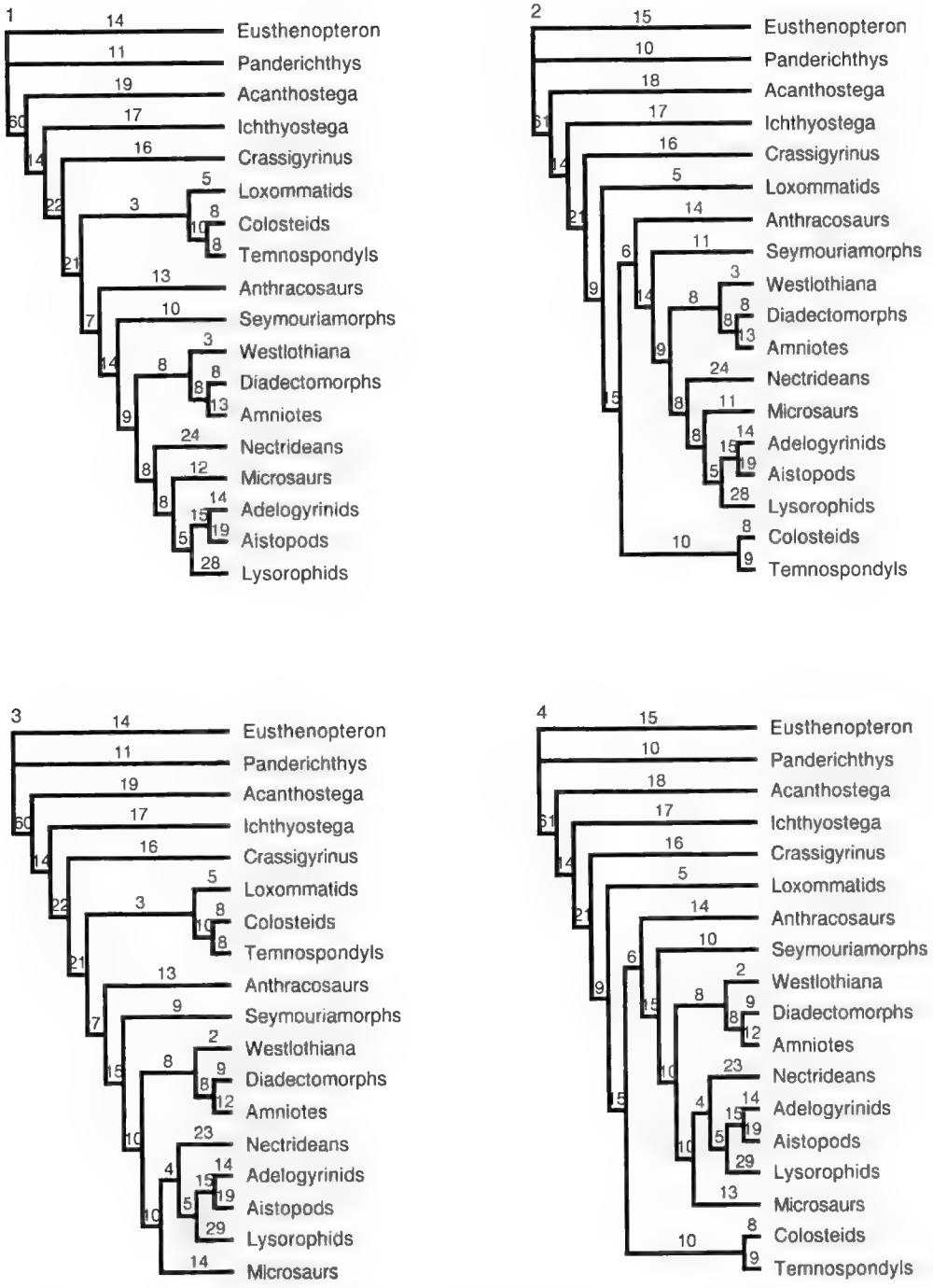


FIG. 8. — The four most parsimonious cladograms generated using the Deltran option, showing branch length.
Les quatre arbres les plus parcimonieux, obtenus avec l'option Deltran, avec la longueur des branches

morphs, amniotes, and the common ancestry of the lepospondyls. The final polytomy involves the common ancestry of adelogyrinids and aïstopods and the remaining lepospondyl groups.

At 458 steps, 116 trees were generated. The resolution between the lepospondyl and amniotes and their immediate sister-groups is lost in the strict concensus, but is still supported in the majority rule (50%) concensus tree. A similar pattern persists at 459 steps (Fig. 9).

Given the latitude (or constraint) of only five steps beyond the most parsimonous tree (less than 1% of the total number of steps), the resolution of post-Devonian tetrapods is greatly reduced, but maintains many informative features. How significant is this 1% increase in the number of steps?

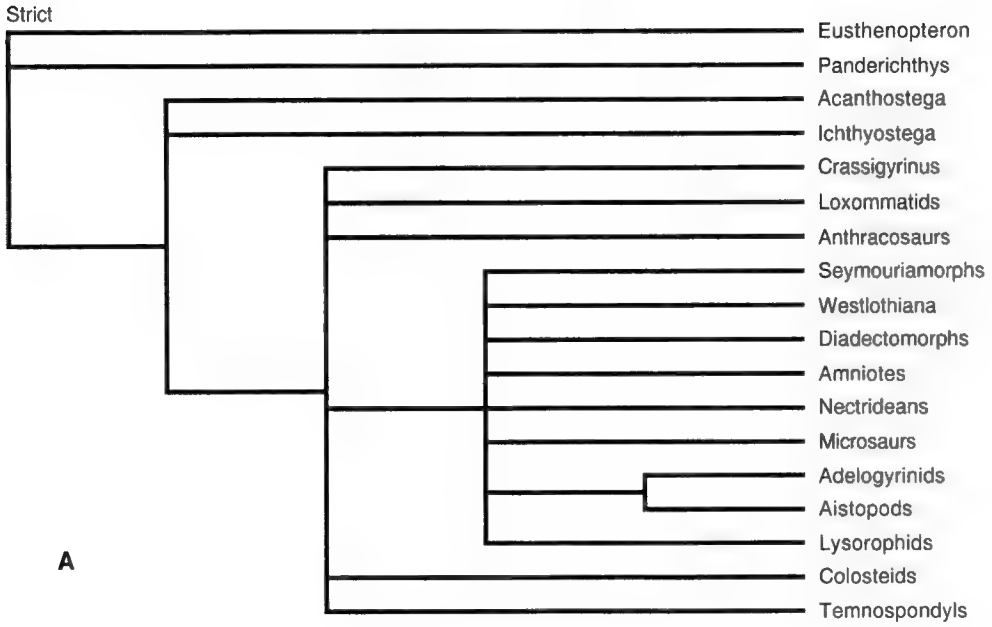
Most systematists are satisfied with achieving full resolution of all taxa (without polytomies) in the most parsimonious cladograms. This assumes that the data set available is representative of the total variability of character states among the taxa involved. In the case of Paleozoic tetrapods, there is considerable evidence that the available information is very incomplete in relationship to the total skeletal variability and the taxonomic diversity of the Paleozoic. The cladograms alone demonstrate the great gap in information of early Carboniferous lineages. If lepospondyls are a natural group (as indicated by nearly every tree generated) the lineages leading to adelogyrinids, microsaurs, nectrideans, and lysorophids must have existed since at least the time of occurrence of the first known lepospondyl, the aïstopod *Lethiscus*, in the mid-Visean. Yet lysorophids, microsaurs, and nectrideans are only known with assurance in the Upper Carboniferous. If seymouriamorphs are the sister-group of both lepospondyls and the amniote assemblage, their immediate ancestors should also be present in the Lower Carboniferous, but are not known with assurance until the Upper Carboniferous, and for the seymouriamorphs, the Lower Permian. There is no direct way to judge the extent of these gaps in terms of missing data, but it is almost certain that the early members of all the lineages were more primitive than their late Carboniferous derivatives that contribute to the known data set.

A more specific measure of the absence of information is provided by the number of question marks in the data set, which amount to approximately 15% of the total data. The number of character states that are unknown is far greater than the number of steps involved in the trees generated.

Systematic generation and analysis of trees beyond 459 steps become time consuming. On the other hand, one can design particular trees to establish how many steps are necessary to achieve specific relationships. For example, the number of additional steps necessary to produce sister-group relationships between particular lepospondyls and particular labyrinthodonts, or between amniotes and various other groups. At six steps beyond the most parsimonious cladogram, seymouriamorphs appear as the sister-group of *Westlothiana*, diadectomorphs, and amniotes to the exclusion of lepospondyls, or *Westlothiana* becomes the sister-group of nectrideans. At ten extra-steps, *Westlothiana* appears as the sister-group of lysorophids. At thirteen extra-steps:

FIG. 9. — A, strict consensus tree generated via Deltran, at five steps more than most parsimonious. B, majority rule (50%) consensus tree generated via Deltran, at five steps more than most parsimonious.

A, arbre consensus strict obtenu avec l'option Deltran, cet arbre a cinq pas de plus que l'arbre le plus parcimonieux. B, arbre consensus, règle de majorité (50%) option Deltran. Cet arbre a cinq pas de plus que l'arbre le plus parcimonieux.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Diadectomorphs
Amniotes
Nectrideans
Microsaurs
Adelogyrinids
Aistopods
Lysorophids
Colosteids
Temnospondyls
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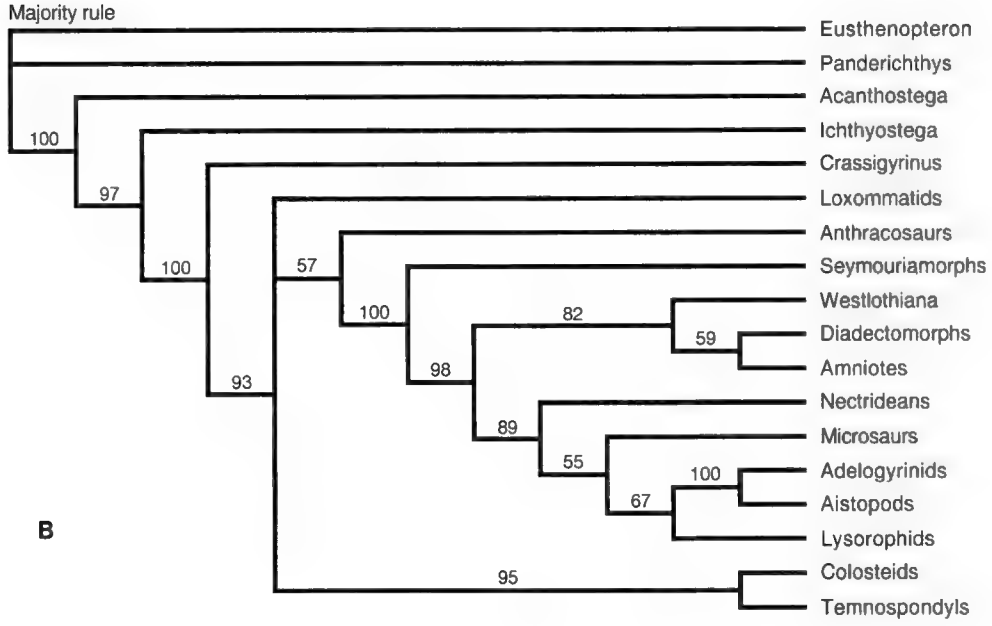
Majority rule
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Anthracosaurs
Seymouriamorphs
Westlothiana
Diadectomorphs
Amniotes
Nectrideans
Microsaurs
Adelogyrinids
Aistopods
Lysorophids
Colosteids
Temnospondyls
100
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98
93
89
55
100
67
95
B

lysorophids are the sister-group of amniotes, diadectomorphs and *Westlothiana*. At 16 – seymouriamorphs and temnospondyls are sister-groups; at 21 – seymouriamorphs and lysorophids; at 28 – anthracosaurs and lysorophids; and at 32 – lysorophids and colosteids. The latter still represents only a 7% increase in the total number of steps.

DELTRAN AND ACCTRAN

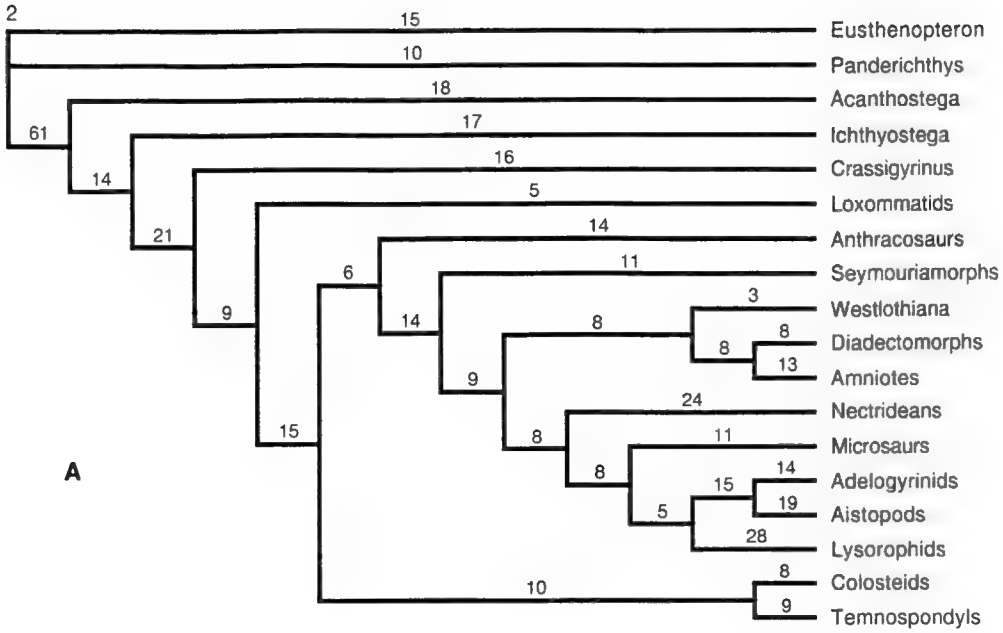
Another way to judge the relative adequacy of this data to determine specific relationships can be gained by comparison of the number and identity of the characters assigned by the alternative options Deltran and Acctran (Fig. 10).

The procedure followed by these options either accelerates or delays the time at which a particular character change is indicated, within the standard parsimony constraints (SWOFFORD, 1993: 20). If two patterns of character distribution are equally parsimonious, but one involves an earlier change in character state than the other, it will be selected by Acctran. Conversely, Deltran delays the time at which the change is expressed in the cladogram. The amount of flexibility in these cladograms is greatly increased by the absence of data, which precludes identification of the specific point in the cladogram where a change must be recognized. Poorly known forms such as loxommatids may occupy a considerable range of positions. There is no difference in the pattern of branching that results from chosing the Deltran or Acctran option, nor the total number of steps in the most parsimonious tree. On the other hand, the number of characters that support each node are very clearly different (table 1). The number of character changes between fish and tetrapods (in tree 2 of the most parsimonious trees) differs from 61 to 88, nearly a 50% increase. This gives a very different impression of the number and nature of character changes that are involved in the origin of tetrapods. At the other end of the scale, some terminal taxa were distinguished by many more steps under Deltran than with Acctran. For example, *Acanthostega* shows 18 apomorphies with Deltran, and 9 with Acctran. Lysorophids show 28 with Deltran and 17 with Acctran. These differences, between trees with globally equal parsimony, is startling. Examination of the apomorphy list showed that not only the number, but the specific characters involved differed significantly depending on the option used.

Omitting the nodes leading to *Eusthenopteron* and *Panderichthys* (which do not differ), the number of character transformations in tree # 2 of the four most parsimonious trees recognized by both Deltran and Acctran totals 292, compared with an additional 270 steps recognized by one or the other option, but not both. This portion of the most parsimonious tree has 429 steps, but only 292 of these transformations are specific to particular nodes. Two hundred and seventy

FIG. 10. — Comparison of branch lengths in the most parsimonious trees generated by A. Deltran, and B. Acctran. Both trees total 454 steps.

Comparaison des longueurs de branches des arbres les plus parcimonieux obtenus par A, option Deltran et B, option Actran. La longueur des arbres est de 454 pas évolutifs.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Amniotes
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Microsaurs
Adelogyrinids
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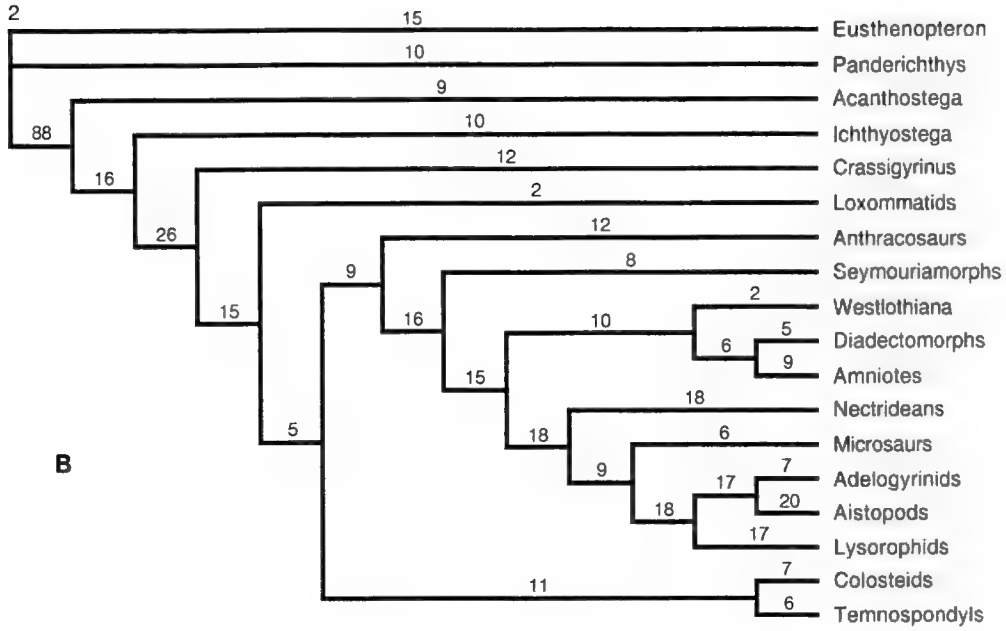
Lysorophids
Colosteids
Temnospondyls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Amniotes
Nectrideans
Microsaurs
Adelogyrinids
Aistopods
Lysorophids
Colosteids
Temnospondyls

transformations may have occurred one or more nodes above or below. That is, 62.9% of the assignments of character state changes are equivocal as to node. These character changes are useful in establishing the geometry of the tree, since it does not differ from Deltan to Acctran, but they can give a very misleading view of what specific changes characterize particular nodes and taxa.

Consideration of particular nodes

This analysis shows a great many character states changes between known osteolepiform fish and the earliest known tetrapods. Sixty or 61 are tabulated in the four most parsimonious cladogram run under Deltran, and 88 in Acctran. These numbers are far in excess of those that occur elsewhere in these cladograms. This certainly reflects a major change in structures throughout the skeleton, and implies major differences in their way of life. Clack & Coates (1995) emphasis that increasing knowledge of *Acanthostega* and *Ichthyostega* are bluring the apparent distinction between fish and tetrapods and that subsequent discoveries are likely to reduce this number until recognition of tetrapod status will depend on formal definitions based on the achievement of particular attributes. However, even discounting all of the possible reversals and homoplastic origin of advanced characters that may occur in early tetrapods, the currently available evidence points to a major reorganization between osteolepiforms and early amphibians.

The taxa *Acanthostega*, *Ichthyostega*, *Crassigyrinus*, and loxommatids appear as progressive steps in a *scala naturae* based on the progressive accumulation of derived characters with little real resolution of interrelationships (see discussion of this problem in Panchen, 1991). The characters cited by Panchen & Smithson (1988) to support specific interrelationships among this assemblage may have greater significance than appears in these trees, but they are swamped by other data.

Too little is yet known of loxommatids for their specific affinities to be established. In the most parsimonious trees, three characters support a node uniting loxommatids with colosteids and temnospondyls, compared with 10 uniting colosteids and temnospondyls to the exclusion of loxommatids; the latter pattern is considered more probable. All other Paleozoic tetrapods appear to belong to two divergent groups, the colosteids and temnospondyls on one hand, and all the rest on the other.

Several papers have proposed a sister-group relationship between temnospondyls and microsaurs (e.g. Smithson, 1985; Milner, 1994). For that reason a search was made to locate trees constrained to show relationships between these groups. Four trees were found with a length no less than 479 steps; 25 steps more than the most parsimonious trees. Four to five characters, showing a great deal of homoplasy elsewhere in the tree, supported their sister-group status. On the basis of the data presented here, the similar derived characters cited by Smithson & Milner must be assumed to be homoplastic (e.g. the shape of the humerus) or primitive (e.g. support of the braincase by contact between the exoccipitals and postparietals) (Carroll & Chorn, 1994). On the other hand, all the cladograms generated strongly support a sister-group relationship between colosteids and temnospondyls.

Seymouriamorphs occupy a crucial position in nearly every cladogram, at the base of a radiation including diadectomorphs and amniotes on one hand and lepospondyls on the other. This phylogenetic hypothesis raises several crucial and interrelated questions.

1 – Are seymouriamorphs a plausable sister-group of amniotes and lepospondyls?
2 – Are lepospondyls a plausable sister-group of amniotes?
3 – Are lepospondyls a natural group?

Critical to this problem is the putative monophyly of lepospondyls. Their unity is recognized up to 4 steps beyond the most parsimonious cladogram. Beyond this level, one or other of the orders may appear as the sister-group of other taxa in some trees, but even in cladograms generated at 25 steps beyond the most parsimonious, the general cohesion of the group is retained.

Despite the consistant unity of lepospondyls reflected in these cladograms, analysis of the supporting characters does not give strong credence to this phylogenetic hypothesis.

The apomorphies of the lepospondyls differ in each cladogram, but in tree 2 of the most parsimonious cladograms, their monophyly is supported by the following synapomorphies according to the Deltran option (node 24).

7. Prefrontal enters narial opening.
12. Loss of squamosal embayment.
57. Loss of retractor pit.
85. Loss of proatlas.
86. Loss of atlas intercentrum.
87. Lateral expansion of atlas centrum.
101. Trunk intercentra lost.
162. Non-bifurcate iliac blade. Only 162 is not also recognized by Acctran.

In Acctran only:

59. Braincase supported by contact of opisthotic and skull roof.
71. Appearance of a short retroarticular process.
84. Broad articulating surface of occiput.
91. Axis intercentrum lost.
100. Capitulum of rib articulates with margin of more anterior centrum.

If lepospondyls are a monophyletic group, it would be expected that the most primitive character states observed in any one subgroup would be plesiomorphic for lepospondyls as a whole, unless there was strong evidence for reversal. For that reason, the presence of a narrow occipital articulation seen in adelogyrinids and aïstopods is presumably primitive for lepospondyls. The presence of a proatlas in aïstopods and lysorophids is much more likely to be a primitive feature of lepospondyls than the result of re-elaboration of this element in two lineages. Adelogyrinids appear to retain a squamosal embayment, but the fusion of the squamosal and the tabular make the homology of this area difficult to evaluate. The bifurcate iliac blade present in microsaurs is almost certainly a primitive feature for that order (since it is lost in Permian genera), and is probably primitive for tetrapods and lost among lepospondyls. The presence of intercentra in some part of the column in microsaurs may be primitive for lepospondyls. In most

lepospondyl groups the braincase is supported by contact between the postparietals and the exoccipitals, a condition that is probably primitive for tetrapods (CARROLL & CHORN, 1994). The condition in some nectrideans of contact between the opisthotic and the skull roof is very unlikely as a synapomorphy of lepospondyls. It is more likely that a retroarticular process evolved within the lepospondyls, rather than being primitive for the group and then being lost. The loss of the retractor pit for the rectus eye muscles seems a very unlikely reversal.

The current study reveals no certain cranial synapomorphies. The entrance of the prefrontal into the narial opening might be primitive for the group, but also occurs in early colosteids. In a recent evaluation of lepospondyl relationships (CARROLL & CHORN, 1994), three vertebral features were recognized as apparent synapomorphies: atlas pleurocentrum formed as a single center of ossification without a distinct atlas intercentrum, proatlas lacking specific articulating surfaces for the external surface of the occiput, single cylindrical trunk centra occupying entire length of segment. If study is concentrated on the lepospondyls, without attempting to integrate the character distribution within this group with that of all other Paleozoic tetrapods to achieve a single most parsimonious pattern, the number of unique derived characters that they all share is very limited, but may indicate a common origin, distinct from that of any other groups of Paleozoic tetrapods.

Within the lepospondyls, the most constant feature of the cladograms is the sister-group position of adelogyrinids and aïstopods. This can certainly be attributed to the common derived condition of limb loss. When the data pertaining to limbs is omitted, adelogryinids and aïstopods assume a variety of positions among the lepospondyls, but this does not alter the unity of the group as a whole. Unfortunately, there is no direct way to judge whether limb loss is homologous in the two groups. The very different pattern of the skulls, and the retention of a primitive pattern of the dermal shoulder girdle in adelogyrinids suggest that limb loss is not homologous but occurred by homoplasy, as in the case a many lineages of limbless lizards (GREER, 1991).

Among the four most parsimonious trees, the geometry of the lepospondyls differs in having either the nectrideans (trees 1 and 3) or the microsaurs (trees 2 and 4) as the sister-group of all other lepospondyls. These differences are based on the timing of the loss of intercentra and supratemporal, the gain and/or loss of a retroarticular process, and changes in the humeral shaft. Either way, a number of reversals must be assumed.

The proposed sister-group relationship between amniotes, *Westlothiana*, and diadectomorphs on one hand and lepospondyls on the other is even more difficult to assess. Node 25 shows the following derived characters as uniting these groups.

4. Lateral line canals not expressed in adults.
23. Loss of intertemporal.
34. Absence of fangs on vomers.
35. Loss of palatal fangs.
38. Loss of labyrinthine infolding.
70. Large, elongate foramina between prearticular, angular, and splenial.
77. Stapes inclined to margin of jaw.
99. Reduced length of transverse processes.
139. Reduction in length of entepicondyle.

All but 34, 70 and 77 are recognized by both Deltran and Acctran.

Acctran also recognizes:

12. Reduction of squamosal embayment.
15. Presence of post-temporal fossa.
44. Cheek vertical.
63. One splenial.
84. Hemispherical occipital condyle.
93. Arch and pleurocentrum of axis fused.
131. Distinct shaft of humerus.
132. Increased torsion of humerus.
150. Presence of pisiform.

Most characters that support these affiliations are subject to a number of reversals, and/or are of uncertain homology. Characters 4, 12, 44, 63, 93, 99, 131, and 150 are probably not present in the most primitive lepospondyls, although they do occur in one or more genera within this group. Character 15 is probably primitive for tetrapods, but changes in *Seymouria* and so must reverse in a transition toward either amniotes or lepospondyls. It is not an appropriate synapomorphy of lepospondyls and the amniote assemblage. The character state change indicated by 84 is subsequently modified among lepospondyls, which have evolved very different patterns of articulation between the occiput and the first cervical. It is not a synapomorphy of the two groups. Labyrinthine infolding (38) is present in the most primitive diadectomorphs. A large opening on the medial surface of the lower jaw (70) is present only sporadically in each group and is an unreliable character for establishing relationships. It appears at this position in a cladogram in which nectrideans are the sister-group of other lepospondyls, but not if this position is assumed by microsaurs.

It has been suggested (CARROLL, 1986a, 1989) that several of the derived features shared by lepospondyls and amniotes may be the result of small size, rather than common ancestry. This applies particularly to the loss of palatal fangs, infolding of the enamel, and loss of some skull bones. The closure of the squamosal notch may have a similar explanation. To test this hypothesis, characters 12, 23, 34, 35, 36, and 38 were removed from the data matrix. However, this did not alter the basic pattern of the four most parsimonious trees, nor the seven generated with one additional step. Among the 28 trees generated at two steps more than the most parsimonious, one showed seymouriamorphs as the sister-group of lepospondyls, and these two as the sister-group of amniotes, diadectomorphs, and *Westlothiana*. Seventy-one trees were generated at three steps beyond most parsimonious. The strict consensus tree showed a polytomy of seymouriamorphs, *Westlothiana*, diadectomorphs, amniotes, and the common ancestor of all the lepospondyl groups. Individual cladograms showed *Westlothiana* as the sister-group of lepospondyls, and as the sister-group of lepospondyls plus diadectomorphs and amniotes, and seymouriamorphs as the sister group of *Westlothiana*, diadectomorphs and amniotes, and these together as the sister-group of lepospondyls, and seymouriamorphs as the sister-group of lepospondyls and these together as the sister-group of diadectomorphs and amniotes. Nevertheless, the basic integrity of the lepospondyls and the unity of *Westlothiana*, diadectomorphs, and amniotes remained despite the removal of these characters.

CARROLL (1989) has also argued that the cylindrical shape of the vertebrae may be convergently achieved among early tetrapods, as it has been in teleosts and lissamphibians. Removal of vertrebral characteristics from the data matrix leaves it so reduced (especially among limbless lepospondyls) as to question the validity of any resulting trees. Resolution of this problem requires discovery of the plesiomorphic sister-groups of both lepospondyls and the amniote assemblage from the earliest Carboniferous to resolve the early stages in the evolution of their vertebral patterns.

This leave only two characters, 77 and 139, that are not either subject to extensive reversals or of dubious homology, to support the sister-group relationship of lepospondyls and the amniote assemblage.

Whether or not lepospondyls and amniotes are sister-groups, there remains the problem of their affinity with seymourimorphs. According to the character change list generated via Deltran, the following synapomorphies identify seymouriamorphs as the sister-group of higher tetrapods.

36. Loss of fangs on ectopterygoid.
43. Distinct epipterygoid.
59. Braincase supported by double articulation between tabular and opisthotic without contribution of stapes.
61. Reduced size of occipital articulation relative to size of foramen magnum.
68. Loss of parasymphysial fangs.
82. Stapes looses contact with palatoquadrate, but impedance matching middle ear not developed.
88. Atlas pleurocentrum cylindrical.
92. Axis pleurocentrum cylindrical.
96. Supraneural canal does not penetrate arch.
102. Trunk pleurocentra cylindrical.
103. Reduced number of presacral vertebrae.
136. Loss of keel of humerus.
137. Separate supinator process.
180. Phalangeal count of pes 2, 3, 4, 5, 4.

All but 103 were also identified by Acctran, which also recognized:

77. Stapes extends toward jaw articulation modified in *Seymouria*.
132. Increased torsion of humerus.
176. Tibiale and intermedium distal to tibia.

Together, this appears as a very convincing list of synapomorphies. The question then arises as to the reliability of character states exhibited by known seymourimorphs to establish relationships with lepospondyls. If seymouriamorphs are the sister-group of lepospondyls (and lepospondyls are a natural group), they must share an immediate common ancestry no later than the mid-Visean, at which time the oldest lepospondyl *Lethiscus* is known. Had the character states that are shared by known seymouriamorphs evolved by that time? In fact, seymouriamorphs are known no earlier than the early Permian, some 60 million years later. Seymouriamorphs are the only major group of tetrapods known in the Lower Permian that have no known representatives

in the Carboniferous. Many character state changes occurred between the Lower Carboniferous and the Lower Permian within other lineages, showing that character states in derived taxa do not necessarily reflect their affinities with other groups that diverged in the Devonian or Lower Carboniferous. For example, the following characters that seymouriamorphs share with amniotes and lepospondyls are also present in advanced, but not primitive anthracosaurs: axis pleurocentrum cylindrical, supraneural canal does not penetrate arch, trunk pleurocentra cylindrical, reduced number of presacral vertebrae. The character states exhibited by Permian seymourimorphs were probably also derived relative to those of their plesiomorphic sister-group, but there is currently no way to know what character states their unknown Carboniferous ancestors may have had. This, however, is simply a matter of uncertainty, and does not provide any evidence contrary to a sister-group relationship with either lepospondyls or amniotes.

A sister-group relationship between amniotes and diadectomorphs is now generally accepted (SUMIDA & LOMBARD, 1991), and is well supported by these cladograms. The most interesting recent discovery that may be associated with the ancestry of amniotes is that of *Westlothiana* from the Brigantian of Scotland (SMITHSON *et al.*, 1993). The most parsimonious cladograms indicate the same phylogentic position as hypothesized by SMITHSON *et al.*, as the sister-group of diadectomorphs and amniotes. This is supported by the following synapomorphies, according to Deltran.

3. Sutural attachment of postfrontal and parietal to postorbital.
12. Loss of squamosal notch.
44. More vertical cheek.
63. One splenial.
95. Arches fused to centrum during development.
104. Two sacral vertebrae.
132. Increased torsion of humerus.
162. Reduced dorsal process of ilium.

Only 3, 95, 104 and 162 are also recognized by Acctran.

Acctran also recognizes:

15. Posttemporal opening between otic capsule, supraoccipital and cheek.
51. Supraoccipital a broad plate of bone closely attached to tabulars and otic capsule loose attachment in amniotes.
60. Hemispherical occipital condyle a critical character, but not actually observed in *Westlothiana*.
64. Two coronoids.
151. Pisiform also not observed in *Westlothiana*.
176. Tibiale, intermedium and centrale distal to tibia.

In the next most parsimonious trees, *Westlothiana* appears also as the sister-group of amniotes, with diadectomorphs as the out-group. At two steps beyond the most parsimonious cladograms, *Westlothiana* is represented as either the sister-group of lepospondyls, or as the sister-group of diadectomorphs to the exclusion of amniotes, or as the sister-group of an assemblage including lepospondyls, diadectomorphs, and amniotes. As elsewhere in the cladogram, it is difficult to

argue for a specific phylogenetic position for this taxon. This may be attributed partially to the fact that 20% of its anatomy remains unknown.

The uncertainties raised by this phylogenetic analysis indicate that we are still very far from establishing a dependable phylogeny of Paleozoic choanates. As argued by DONAGHUE *et al.* (1989), this can only be accomplished by a better knowledge of the more plesiomorphic sister-groups of all the taxa in question.

SUMMARY AND CONCLUSIONS

Phylogenetic analysis has been performed on a large data set representative of the entire skeleton of all major groups of Paleozoic tetrapods. Fully resolved cladograms result in a sequence of labyrinthodont groups that are successive sister-groups of an assemblage including seymouriamorphs as the sister-group of two clades, the lepospondyls on one hand and *Westlothiana*, diadectomorphs and amniotes on the other. Up to five steps beyond the most parsimonious cladogram, there is strong support for a sequence of progressively more derived labyrinthodonts groups in the order *Acanthostega*, *Ichthyostega*, *Crassigyrinus*, loxommatids, anthracosaurs and seymouriamorphs. The affinities of colosteids and temnospondyls is strongly supported but this clade may appear either below or (rarely) above the position of the anthracosaurs. The lepospondyls and the clade including *Westlothiana*, diadectomorphs, and amniotes maintain their integrity at a level five steps beyond the most parsimonious trees.

Running the data alternatively with the Deltran and Acctran options shows that more than 60% of the character state changes cannot be specified as occuring at particular nodes. This ambiguity results from missing data. This can be attributed to two major factors: (1) lack of at least some data from all known taxa; (2) lack of any information of more plesiomorphic members of recognized clades that must have been present during the 30 million years of the Lower Devonian and Early Carboniferous, but are not known from the fossil record.

In the absence of data from more plesiomorphic members of the major groups, it is not possible to determine what derived characters were present in the earliest members of these clades, or whether or not similar characters in different clades are homologous. This is particularly crucial in the case of seymouriamorphs which lack any Carboniferous representative, but appear as the sister-group of both lepospondyls and the clade including amniotes, both of which must have diverged early in the Lower Carboniferous.

The presence of numerous reversals, questionable homologies, and the scarcity of well established synapomorphies cast doubts on the acceptance of the lepospondyls as a monophyletic clade and on the sister-group status of lepospondyls and the assemblage including *Westlothiana*, diadectomorphs and amniotes.

No matter how cogent the underlying theories of phylogenetic systematics, or how effective the computer software, there is no way to produce a reliable phylogeny in the absence of dependable data. In the case of the radiation of early tetrapods, the almost complete absence of data from the first 25 million years of the Carboniferous makes it extremely difficult to determine character states in the most plesiomorphic members of these clades that can be used to establish

sister-group relationships. The only solution to this problem is to discover and describe fossils from this crucial stage in the evolution of vertebrates.

The data matrix presented here, should, nevertheless, provide a useful framework for subsequent work on the phylogeny of early tetrapods. It provides a means of characterizing each particular clade, and for demonstrating what changes have occurred from one group to another.

The cladograms presented here should be recognized as a representation of the most parsimonious distribution of known character states, rather than of the biological relationship of the taxa. PAUP and other computer packages are a convenient way to manipulate data, but there is no way in which they can determine whether or not characters are homologous, or whether particular transformations are biologically probable. SCOTT & JANIS (1993: 300) have discussed this and related problems in a forceful, but humorous style, concluding, "... computer programs, ... like the White Queen, can believe six impossible things before breakfast".

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TABLE 1. — Comparison of number of character state changes recognized by Acctran and Deltran.
Tableau comparatif du nombre de changements d'états de caractères reconnus par les options Acctran et Deltran.

Node	Character transformations recognized by both Deltran and Acctran	Character transformations recognized by either Deltran or Acctran, but not both
34 --> 33	61	27
33 --> *Acanthostega*	9	9
33 --> 32	10	10
32 --> *Ichthyostega*	6	15
32 --> 31	15	17
31 --> *Crassigyrinus*	10	8
31 --> 30	6	12
30 --> Loxommatids	2	1
33 --> 29	3	14
29 --> 27	4	7
27 --> Anthracosaurs	9	8
27 --> 26	13	4
26 --> Seymouriamorphs	7	5
26 --> 25	6	12
25 --> 20	4	10
20 --> *Westlothiana*	2	1
20 --> 19	2	10
19 --> Diadectomorphs	4	5
19 --> Amniotes	9	4
25 --> 24	7	12
24 --> Nectrideans	16	10
24 --> 23	3	11
23 --> Microsaurs	4	9
23 --> 22	4	15
22 --> 21	15	2
21 --> Adelogyrinids	7	7
21 --> Aïstopods	18	3
22 --> Lysorophids	16	13
29 --> 28	8	3
28 --> Colosteids	6	3
28 --> Temnospondyls	6	3

APPENDIX I

Distribution of character states in Paleozoic choanate vertebrates.
Data marked with * (pers. comm., Drs CLACK and COATES).

PRIMITIVE CHOANATE CONDITION	DERIVED CONDITION
SKULL KINESIS	
1-0. Mobility between anterior and posterior elements of skull table	1-1. Interdigitating sutures connect; parietal and intertemporal with postparietal and supratemporal; (*Panderichthys* and all tetrapods);
2-0. Mobility between lacrimal and prefrontal	2-1. Mobility lost (*Panderichthys*, all tetrapods except early nectrideans);
3-0. Mobility between skull table and cheek lateral to postfrontal, intertemporal, supratemporal, and tabular	3-1. Sutural attachment of postfrontal and intertemporal with postorbital (*Panderichthys*);
	3-2. Sutural attachment of parietal and supratemporal to postorbital and squamosal (*Acanthostega*);
	3-3. Sutural attachment of postfrontal, parietal, supratemporal, and tabular to postorbital and squamosal (*Ichthyostega*);
	3-4. Sutural attachment of postfrontal, intertemporal, and supratemporal to postorbital squamosal (loxommatids, seymouriamorphs, temnospondyls);
	3-5. Sutural attachment of postfrontal and parietal to postorbital (*Westlothiana*, diadectomorphs and amniotes);
	3-6. Sutural attachment of parietal to postorbital, mobility between postorbital and jugal (nectrideans);
	3-7. Sutural attachment of postfrontal, (parietal) and tabular to postorbital and squamosal (microsaurs);
	3-8. Sutural attachment of postfrontal and tabular-squamosal to jugal and quadratojugal (adelogyrinids);
	3-9. Sutural attachment of parietal and tabular to squamosal (lysorophids);
	3-a. Sutural attachment of postfrontal, parietal, (intertemporal), supratemporal, and tabular to postorbital and squamosal (colosteids);
LATERAL LINE CANALS	
4-0. Primitive configuration shown in figure 1B	4-1. Lateral line canals not expressed in adults (*Westlothiana*, ? diadectomorphs, amniotes, microsaurs, lysorophids, nectrideans, aïstopods);

5-0. Canals surrounded by bone	5-1. If present, canals exposed superficially (all tetrapods except *Devonian genera*);
SKULL OPENINGS	
6-0. Single narial opening on lateral surface of snout	6-1. Narial opening facing ventrally (*Panderichthys, Acanthostega, Ichthyostega*, primitive anthracosaurs); 6-2. Secondarily lateral position (all tetrapods except 6-1);
7-0. Nasal openings bordered by anterior rostral and lateral tectal	7-1. Opening bordered by anterior tectal, premaxilla, and maxilla (*Acanthostega*); 7-2. Opening bordered by anterior tectal, lateral rostral, premaxilla and maxilla (*Ichthyostega*); 7-3. Opening bordered by premaxilla, maxilla and lacrimal (anthracosaurs); 7-4. Opening bordered by premaxilla, maxilla, lacrimal, nasal, and septomaxilla (loxommatids, seymouriamorphs, *Westlothiana*, diadectomorphs; amniotes, temnospondyls, and ? adelogyrinids); 7-5. Opening bordered by premaxilla, maxilla, lacrimal, nasal, prefrontal (? microsaurs, nectrideans, lysorophids, aïstopods, colosteids);
8-0. Pineal opening surrounded by several small pineal plates	8-1. Loss of pineal plates (*Panderichthys* and all tetrapods); 8-2. Loss of pineal opening (lysorophids);
9-0. Orbits facing laterally	9-1. Orbits close to midline and facing dorsally (*Panderichthys, Crassigyrinus*);
10-0. Bones surrounding orbit: pre– and postfrontal, postorbital, jugal, and lacrimal	10-1. Pre-and postfrontal, postorbital, and jugal (*Ichthyostega, Acanthostega, Crassigyrinus*); 10-2. Frontal, pre- and postfrontal, postorbital, jugal, lacrimal (amniotes); 10-3. Prefrontal, lacrimal, maxilla, palatine, squamosal, parietal (lysorophids); 10-4. Pre- and postfrontal, jugal, lacrimal (adelogyrinids); 10-5. Pre– and postfrontal, jugal, maxilla, lacrimal (aïstopods);
11-0. Orbit, round, oval, or rhomboidal	11-1. Keyhole shaped (loxommatids); 11-2. Open posteriorly (lysorophids);
12-0. Narrow slit for spiracle between squamosal, tabular and supratemporal	12-1. Squamosal embayment bordered by tabular and squamosal (*Ichthyostega, Acanthostega*); 12-2. Squamosal embayment bordered by tabular, supratemporal, and squamosal (*Crassigyrinus*, loxommatids, anthracosaurs, seymouriamorphs);

	12-3. Squamosal and supratemporal modified to support tympanum (temnospondyls); 12-4. Notch reduced to slit between supratemporal and squamosal (*Westlothiana*, diadectomorphs, amniotes); 12-5. Embayment in tabular squamosal (adelogyrinids); 12-6. Loss of embayment (microsaurs, nectrideans, lysorophids, aïstopods, colosteids);
13-0. Cheek fully ossified	13-1. Postfrontal, postorbital, and jugal lost to form large opening confluent with orbit (lysorophids); 13-2. Large open space between squamosal and postorbital and jugal covered with osteoderms (aïstopods);
14-0. Mouth terminal	14-1. Mouth subterminal (*Panderichthys*);
15-0. Large openings in occiput for fossa bridgei	15-1. Fenestrae for fossa bridgei reduced to small post-temporal fossae, passing between; otic capsule and tabular and postparietal (loxommatids, temnospondyls, colosteids, microsaurs, ? aïstopods); 15-2. No openings (anthracosaurs, *Crassigyrinus*, seymouriamorphs); 15-3. Post-temporal fossae between otic capsule, supraoccipital and cheek (diadectomorphs, amniotes); 15-4. Post-temporal fossae between otic capsule, exoccipital, and postparietal (the nectridean *Diplocer-aspis*); 15-5. Opening between otic capsule and tabular squamosal (adelogyrinids); 15-6. Opening between exoccipital, postparietal and supraoccipital (lysorophids);

INDIVIDUAL BONES OF SKULL ROOF

16-0. Mosiac of numerous rostrals	16-1. Single pair of rostrals (internasals) (*Acanthostega* and loxommatids); 16-2. Median rostral (*Ichthyostega*); 16-3. Opening in skull between premaxillae and nasals (*Crassigyrinus*); 16-4. Elimination of rostrals (all other tetrapods);
17-0. Presence of lateral rostral	17-1. Loss of lateral rostral, or modification of this bone to septomaxilla (all tetrapods except *Ichthyostega* and *Crassigyrinus*);

18-0. Presence of anterior tectal	18-1. Loss of anterior tectal (all tetrapods except *Ichthyostega, Acanthostega,* and *Crassigyrinus,* ? loxommatids);
19-0. Presence of preopercular	19-1. Absence of preopercular (all tetrapods except *Ichthyostega, Acanthostega,* and *Crassigyrinus*);
20-0. Squamosal reaches maxilla, separating jugal from quadratojugal	20-1. Jugal and quadratojugal in contract separating squamosal and maxilla (some specimens of *Panderichthys* and all tetrapods);
21-0. Maxilla reaches quadratojugal	21-1. Jugal reaches jaw margin, separating excluding jugal from skull marginquadratojugal and maxilla (early anthracosaurs, seymouriamorphs, *Westlothiana*, diadectomorphs, amniotes, ? nectrideans, microsaurs);
22-0. Quadratojugal present	22-1. Loss of quadratojugal (lysorophids);
23-0. Presence of intertemporal	23-1. Loss of intertemporal (the panderichthyid *Elpistostege*, Devonian tetrapods, most loxommatids, most temnospondyls, all microsaurs, aïstopods, nectrideans, adelogyrinids, *Acherontiscus*, *Westlothiana*, diadectomorphs, amniotes);
24-0. Tabular separated from parietal by supratemporal	24-1. Tabular in contact with parietal in presence of distinct supratemporal; (most anthracosaurs, seymouriamorphs, *Westlothiana*, diadectomorphs, amniotes, nectrideans);
	24-2. Tabular in contact with parietal in absence of separate supratemporal (microsaurs, lysorophids, adelogyrinids);
25-0. Posterior margin of tabular forms straight line or gently curved surface with postparietal	25-1. Posterior extension of tabular lateral to an embayment (*Acanthostega*);
	25-2. Conspicuous tabular horn (anthracosaurs, ? *Crassigyrinus*);
	25-3. Posterior extension in conjunction with fused squamosal (adelogyrinids);
26-0. Supratemporal present	26-1. Supratemporal absent (microsaurs, lysorophids, adelogyrinids);
27-0. Postparietal paired	27-1. Postparietals fused at midline (*Ichthyostega*, diadectomorphs);
28-0. Three extrascapular bones	28-1. Loss of extrascapulars (all tetrapods);
29-0. Operculum, consisting of opercular, subopercular, and submandibular plates	29-1. All bones lost in tetrapods except for subopercular in *Ichthyostega*;

PALATE

30-0. Unpaired anterior palatal recess between premaxillae and vomers	30-1. Paired recesses (*Acanthostega*; the colosteid *Greererpeton*);

	30.2. Loss of recess (all tetrapods except; *Ichthyostega*, *Crassigyrinus*, and loxommatids);
31-0. No interpterygoid vacuity	31-1. Large interpterygoid vacuities (temnospondyls, colosteids);
32-0. Premaxilla and maxilla form a straight line lateral to the choana	32-1. Maxilla curves medially and is loosely, if at all, attached to premaxilla (*Panderichthys*, *Ichthyostega*, *Acanthostega*, early anthracosaurs);
33-0. Premaxilla forms border of choana	33-1. Premaxilla attached to vomer, excluded from margin of choana (*Ichthyostega*, *Crassigyrinus**);
34-0. Large fang and pit pairs on vomers	34-1. Absence of fangs on vomers (anthracosaurs, *Westlothiana*, diadectomorphs, amniotes, microsaurs, nectrideans, adelogyrinids, lysorophids, aïstopods);
35-0. Large fang and pit pairs on palatine	35-1. Absence of fangs on palatine (*Westlothiana*, diadectomorphs, amniotes, nectrideans, microsaurs, adelogyrinids, lysorophids, aïstopods);
36-0. Large fang and pit pairs on ectopterygoid	36-1. Absence of fangs on ectopterygoid (*Acanthostega*, seymouriamorphs, *Westlothiana*, diadectomorphs, amniotes, nectrideans, microsaurs, adelogyrinids, lysorophids, aïstopods);
37-0. Row of denticles lateral to palatal fangs, bordering the choana and meeting at the midline of the vomers;	37-1. Absence of denticle row (all tetrapods except *Acanthostega*, *Crassigyrinus**);
38-0. Labyrinthine infolding of dentine	38-1. Absence of infolding (*Westlothiana*, amniotes, nectrideans, microsaurs, lysorophids, adelogyrinids, aïstopods);
39-0. Parasphenoid not covering ventral cranial fissure	39-1. Parasphenoid extending only a short distance across fissure (*Acanthostega* and *Crassigyrinus*);
	39-2. Parasphenoid covering much of basioccipital (all other tetrapods);
40-0. Teeth of upper and lowr jaw of approximately the same size	40-1. Conspicuously larger teeth in dentary than maxilla (colosteids, temnospondyls);
	40-2. Canine teeth in maxilla (amniotes);
41-0. Base of otic-occipital covered by parotic plates	41-1. Loss of parotic plates (all tetrapods);
42-0. Endochondral palatoquadrate articulating anteriorly with olfactory capsule	42-1. Loss of articulation between palatoquadrate and olfactory capsule (all tetrapods);
43-0. Palatoquadrate incorporating epipterygoid	43-1. Distinct epipteryoid (all tetrapods except Devonian genera, *Crassigyrinus*, loxommatids, primitive anthracosaurs and colosteids);
	43-2. Loss of epipterygoid (lysorophids, ? aïstopods);

44-0. Cheek slopes posteriorly, jaw articulation behind occipital condyle	44-1. Cheek more vertical, jaw articulation approximately at level of occipital condyle (*Westlothiana*, diadectomorphs, amniotes, microsaurs, adelogyrinids); 44-2. Jaw articulation significantly anterior to occipital condyle (lysorophids);
45-0. Jaw suspensorium continuous with cheek	45-1. Jaw suspensorium consisting of tabular and squamosal angling forward from skull table (lysorophids); 45-2. Suspensorium consisting of squamosal and quadratojugal, angling posteriorly from skull table (aïstopods);
46-0. Presence of ectopterygoid	46-1. Absence of ectopterygoid (lysorophids);
47-0. Pterygoid extends in a continuous	47-1. Quadrate ramus of pterygoid deeply curve around adductor fossa embayed; to form transverse flange without teeth (seymouriamorphs); 47-2. Transverse flange bears a row of denticles (diadectomorphs and amniotes);
48-0. Palatoquadrate articulates freely with base of braincase via basicranial articulation	48-1. Restriction of mobility of palate and base of braincase (colosteids, temnospondyls, microsaurs); 48-2. Loss of articulating surface on pterygoid (adelogyrinids, lysorophids);

BRAINCASE

49-0. Anterior ethmoid and posterior	49-1. Loss of articulation (all tetrapods); otic-occipital appears capable of; articulation;
50-0. Both portions of braincase ossified as single elements	50-1. Exoccipital, basioccipital, opisthotic, and prootic separately ossified (all tetrapods except aïstopods, condition in *Ichthyostega*, *Acanthostega* not described);
51-0. No separate supraoccipital	51-1. Supraoccipital a broad plate of bone closely attached to tabulars and otic capsule (diadectomorphs); 51-2. Supraoccipital a broad plate of bone loosely attached to the postparietals and separating them from the exoccipitals (amniotes); 51-3. Supraoccipital a narrow ossification beneath skull roof, not separating postparietals from exoccipitals (microsaurs); 51-4. Supraoccipital reaching parietals between postparietals, not separating postparietals from exoccipitals (lysorophids);
52-0. Nasal capsule fully ossified	52-1. Posterior and lateral wall not ossified (*Panderichthys*); 52-2. No ossification of nasal capsule (all tetrapods);

53-0. Basicranial process for articulation with palate on ethmoid element

53-1. Basicranial processes on basisphenoid (all tetrapods);

54-0. Lateral commissure forms stout ridge lateral to otic capsule and surrounds jugular canal

54-1. Loss of lateral commissure (all tetrapods in which braincase is known);

55-0. Two surfaces for articulation hyomandibular on lateral commissure

55-1. Oval head of stapes articulates with margins of fenestra ovalis of otic capsule (all known tetrapods);

56-0. Large unossified area on ventrolateral wall of otic capsule

56-1. Ossification of lateral wall except for area of fenestra ovalis (all tetrapods in which otic capsule is known);

57-0. Eye muscles not originating from a retractor pit

57-1. Retractor pit in basisphenoid (anthracosaurs, seymouriamorphs, diadectomorphs, and amniotes);

58-0. Absence of pleurosphenoid

58-1. Pleurosphenoid extending from basisphenoid (lysorophids, some microsaurs);

59-0. Braincase attached to back of skull via grooves for otic capsule in tabular

59-1. Back of braincase attached to skull roof by processes from postparietal, not comparable to later tetrapods (*Ichthyostega*);

59-2. Braincase support via double articulation between tabular and opisthotic plus stapes (early anthracosaurs);

59-3. Braincase supported via double articulation between tabular and opisthotic (seymouriamorphs, *Westlothiana*);

59-4. Braincase supported by double articulation between tabular and opisthotic plus supraoccipital (diadectomorphs);

59-5. Braincase supported by loose connection between supraoccipital and postparietal (amniotes);

59-6. Braincase supported by contact of opisthotic with both tabular and postparietal (loxommatids);

59-7. Braincase supported by contact between exoccipitals and postparietals, as well as stapes (colosteids);

59-8. Braincase supported by contact of opisthotics and skull roof (nectrideans);

59-9. Otic capsule attached via exoccipital, supraoccipital, and tabular (microsaurs);

59-a. Braincase supported by exoccipital and squamosal tabular (adelogyrinids);

59-b. Braincase supported by otic capsule to supraoccipital, postparietal and cheek (lysorophids);

59-c. Braincase supported by contact of postparietals and exoccipitals (temnospondyls);

60-0. Otic-occipital element of braincase penetrated by notochord, which extends to ethmoid	60-1. Notochord does not extent to ethmoid (all tetrapods except *Ichthyostega*); 60-2. Occiput penetrated by circular pit for notochord (aïstopods); 60-3. Basioccipital deeply penetrated by notochord (*Acanthostega, Crassigyrinus*); 60-4. Basioccipital recessed for first cervical (loxommatids, anthracosaurs, colosteids seymouriamorphs, temnospondyls, microsaurs, lysorophids, adelogyrinids); 60-5. Basioccipital does not contribute to articulation with first cervical (nectrideans); 60-6. Hemispherical occipital condyle (diadectomorphs, amniotes);
61-0. Surface of occiput for articulation with anterior cervicals much larger in vertical extent than foramen magnum	61-1. Surface of occiput for articulation with first cervical significantly smaller; in vertical extent than foramen magnum (seymouriamorphs, diadectomorphs, amniotes, nectrideans, microsaurs, lysorophids, adelogyrinids, aïstopods);

LOWER JAW

62-0. Dentary extends to articular, surangular not reaching margin of jaw	62-1. Long exposure of surangular between dentary and articular (all tetrapods except *Ichthyostega*);
63-0. Two splenials	63-1. One splenial (*Westlothiana*, diadectomorphs, amniotes, nectrideans, aïstopods); 63-2. No splenial (lysorophids);
64-0. Three coronoids	64-1. Two coronoids (diadectomorphs, amniotes); 64-2. One coronoid (nectrideans); 64-3. No coronoids (lysorophids);
65-0. Large coronoid fangs	65-1. Absence of coronoid fangs (all tetrapods except *Crassigyrinus*);
66-0. Pits in coronoids to accommodate palatal fangs	66-1. Pits between coronoids (*Panderichthys);* 66-2. Pits in dentary above coronoids (*Crassigyrinus*); 66-3. Pits in coronoids lost (all other tetrapods);
67-0. Parasymphysial (adsymphysial) plate	67-1. Loss of parasymphysial tooth plate (all tetrapods except *Ichthyostega* and primitive anthracosaurs);
68-0. Parasymphysial fangs *Panderichthys*	68-1. Absence of parasymphysial fangs, (Eusthenopteron, most anthracosaurs, seymouriamorphs, *Westlothiana*, diadectomorphs, amniotes, nectrideans, microsaurs, adelogyrinids, lysorophids, aïstopods);

69-0. Meckelian bone	69-1. Loss of meckelian bone (all tetrapods except *Ichthyostega*);
70-0. Several small openings below margin of prearticular	70-1. Series of small openings in splenials and/or angular (loxommatids, temnospondyls); 70-2. Small openings along suture between prearticular and angular and splenial and postsplenial (seymouriamorphs); 70-3. Large elongate fenestra between prearticular, angular, and splenial (*Limnoscelis*, nectrideans, aïstopods, colosteids); 70-4. Single small opening between splenial and angular (amniotes); 70-5. Small foramen between prearticular and angular (microsaurs); 70-6. No foramina (lysorophids);
71-0. Absence of retroarticular process	71-1. Short retroarticular process (nectrideans, adelogyrinids, lysorophids);
72-0. Conspicuous open lateral line canal between dentary and infradentary bones	72-1. Absence of this canal (all tetrapods except *Acanthostega*);
73-0. Median and principal gular plates	73-1. Loss of gular plates (all tetrapods);

VISCERAL ARCHES

74-0. Hyomandibular large relative to major cranial structures	74-1. Stapes greatly reduced in relative size (all tetrapods);
75-0. Narrow and elongate	75-1. Shortened (all tetrapods);
76-0. No separate dorsal process	76-1. Separate dorsal process (amniotes and some microsaurs);
77-0. Extends posterolatero-ventrally toward jaw articulation	77-1. Toward top of quadrate ramus of pterygoid (*Acanthostega*, colosteids, early anthracosaurs); 77-2. To notch in tabular (*Seymouria*);
78-0. Contacts operculum via opercular facet, to inside of cheek via preopercular facet, to stylohyal	78-1. These contacts lost (all tetrapods);
79-0. Proximal groove for truncus hyoideo-mandibularis of VII nerve	79-1. Loss of this canal (*Panderichthys*, all tetrapods);
80-0. No canal for stapedial branch of orbital artery	80-1. Stapes penetrated by stapedial artery (all tetrapods); 80-2. Secondary loss of stapedial foramen (seymouriamorphs, some microsaurs, lysorophids, aïstopods);

81-0. Complex link between braincase, cheek, and operculum, associated with respiration and feeding	81-1. Role of hyomandibular associated with feeding much reduced or lost (all tetrapods);
82-0. Elongate hyomandibular links palatoquadrate and otic capsule	82-1. Stapes reduced in size, but links otic capsule with palatoquadrate (*Acanthostega*, primitive anthracosaurs, colosteids); 82-2. Stapes loses broad contact with palatoquadrate but not incorporated in an impedance matching system (all other early tetrapods except temnospondyls); 82-3. Incorporation of the stapes in an impedance matching middle ear (temnospondyls);
83-0. Fully ossified complex of five branchial arches, including medial basibranchial(s), paired hypohylals, ceratohyals, hypobranchials, and ceratobranchials ventrally, and epibranchials, infrapharyngobranchials, and suprapharyngobranchials dorsally. In *Eusthenopteron* all covered by dermal dental plates	83-1. Dental plates and infrapharyngobranchials lost variable reduction in other elements (see figure 6) (all tetrapods);

AXIAL SKELETON

VERTEBRAE

Three paired elements per segment: neural arches, dorsal posterior pleurocentra, and ventral anterior intercentra	
84-0. No specialized articulation abut between occiput and cervical vertebra	84-1. Margins of amphicoelous first centrum against conical recess in occiput (aïstopods); 84-2. Central elements of first cervical fit into circular depression formed by exoccipitals and basioccipital (*Crassigyrinus*, anthracosaurs, seymouriamorphs, colosteids, temnospondyls); 84-3. Elements of atlas surround hemispherical occipital condyle (diadectomorphs, amniotes); 84-4. Narrow condyle of first cervical fits into a recess in basioccipital (adelogyrinids); 84-5. Broadened anterior articulating surface of first cervical articulates with strap-shaped surface of basioccipital and exoccipitals (microsaurs and lysorophids);

	84-6. Broadened anterior articulating surface of first cervical articulates with exoccipitals, but not basioccipital (nectrideans);
85-0. No separate element between first cervical vertebra and occiput	85-1. Paired proatlantal elements articulate with occiput and/or atlas arch (*Crassigyrinus*, anthracosaurs, seymouriamorphs, diadectomorphs, amniotes, colosteids, temnospondyls, lysorophids);
	85-2. Median "proatlas" linking occiput and first cervical (aïstopods);
	85-3. Secondary loss of proatlas (adelogyrinids,microsaurs, nectrideans);
86-0. First cervical vertebra has separate crescentic or paired intercentum	86-1. Intercentrum of first cervical lost or incorporated into pleurocentrum (nectrideans, microsaurs, adelogyrinids, lysorophids, aïstopods);
87-0. First centrum no wider anteriorly than more posterior cervicals	87-1. Articulating surface of first centrum expanded laterally (nectrideans, microsaurs, lysorophids);
88-0. Pleurocentrum of first cervical paired	88-1. Atlas pleurocentrum cylindrical vertebra (seymouriamorphs, diadectomorphs, amniotes, nectrideans, microsaurs, adelogyrinids, lysorophids, aïstopods);
89-0. First cervical arch not specialized	89-1. Atlas arch paired, smaller than axis arch (*Acanthostega*, *Crassigyrinus*, anthracosaurs, seymouriamorphs, diadectomorphs, amniotes, colosteids, temnospondyls, adelogyrinids, microsaurs, lysorophids);
	89-2. Atlas arch fused dorsally (nectrideans, aïstopods);
90-0. First cervical arch loosely attached to centrum	90-1. Arch and pleurocentrum of first cervical vertebra fused (nectrideans, aïstopods);
91-0. Intercentrum of second cervical not fused to centrum of first cervical	91-1. Intercentrum of axis fused to atlas centrum (diadectomorphs);
	91-2. Axis intercentrum apparently lost (adelogyrinids, lysorophids, nectrideans, aïstopods);
92-0. Pleurocentrum of second cervical paired	92-1. Pleurocentrum of first cervical lost (*Panderichthys*);
	92-2. Pleurocentrum of axis cylindridal (seymouriamorphs, diadectomorphs, amniotes, microsaurs, adelogyrinids, lysorophids, nectrideans, aïstopods);
93-0. Second cervical arch loosely attached to centrum	93-0. Arch and pleurocentrum of second cervical vertebrae fused (diadectomorphs, amniotes, nectrideans, aïstopods);
94-0. Neural arches of trunk paired	94-1. Neural arches of trunk fused at midline (all tetrapods except *Crassigyrinus*, lysorophids);

95-0. Neural arches not firmly attached centra	95-1. Paired neural arches suturally attached to crescentic intercentra (*Panderichthys*); 95-2. Neural arches articulate with crescentic intercentra (*Acanthostega**, *Ichthyostega*); 95-3. Arches closely articulating with pleurocentra (anthracosaurs, seymouriamorphs, colosteids, temnospondyls, adelogyrinids, lysorophids, some microsaurs); 95-4. Arches become fused to centra during development (*Westlothiana*, ? diadectomorphs, amniotes); 95-5. Arches indistinguishably fused to cylindrical centra even in early stages of development (nectrideans, aïstopods);
96-0. Canal for supraneural ligament penetrates neural arch	96-1. Supraneural canal does not penetrate arch (temnospondyls, advanced anthracosaurs, seymouriamorphs, *Westlothiana*, diadectomorphs, amniotes, nectrideans, microsaurs, adelogyrinids, ? lysorophids, aïstopods);
97-0. Neural arches lack zygapophyses	97-1. Prezygapophyses, but not postzygapophyses (*Crassigyrinus*); 97-2. Pre-and postzygapophyses (all early tetrapods except *Acanthostega**, *Crassigyrinus*);
98-0. Neural arches lack accessory	98-1. Accessory articulating surfaces articulating surfaces (*Acanthostega*, nectrideans, advanced aïstopods);
99-0. Long transverse process extending from arch	99-1. Transverse process short (microsaurs, lysorophids, nectrideans, aïstopods, *Westlothiana*, diadectomorphs, amniotes); 99-2. Transverse process extending from centrum (nectrideans);
100-0. Intercentrum serves for articulation with capitulum of rib	100-1. Capitulum of rib articulates with margin of more anterior centrum (adelogyrinids, microsaurs, lysorophids); 100-2. Capitulum articulation near anterior margin of same centrum (aïstopods, nectrideans);
101-0. Intercentra paired at least in some regions of column	101-1. Intercentra fused ventrally in posterior but not anterior trunk region (*Acanthostega**); 101-2. Intercentra, if present, fused ventrally in all trunk regions (*Panderichthys*, and all tetrapods except *Acanthostega*); 101-3. Trunk intercentra absent (nectrideans, most microsaurs, adelogyrinids, lysorophids, aïstopods);

102-0. Pleurocentra paired	102-1. Pleurocentra crescentic to horseshoe shaped (primitive anthracosaurs); 102-2. Pleurocentra cylindrical (advanced anthracosaurs, seymouriamorphs, *Westlothiana*, diadectomorphs, amniotes, nectrideans, microsaurs, adelogyrinids, lysorophids, aïstopods, *Acherontiscus*); 102-3. Pleurocentra absent (*Panderichthys*, *Crassigyrinus*, loxommatids);
103-0. Between 30 and 42 presacral vertebrae	103-1. 20-29 presacrals (*Ichthyostega*, seymouriamorphs, nectrideans, microsaurs, diadectomorphs, temnospondyls); 103-2. 70 or more (adelogyrinids, lysorophids, aïstopods);
104-0. No sacral vertebrae	104-1. 1 sacral (anthracosaurs, seymouriamorphs, colosteids, temnospondyls, nectrideans, microsaurs, lysorophids); 104-2. 2 sacrals (*Westlothiana*, diadectomorphs, amniotes); 104-3. Sacrals secondarily lost (adelogyrinids, aïstopods);
105-0. Haemal arches present, not fused to centra	105-1. Haemal arches lost (aïstopods); 105-2. Haemeal arches fused to centra (nectrideans);

RIBS

106-0. Ribs very short, linking neural arch and intercentrum	106-1. Ribs much more elongate (all tetrapods except *Acanthostega*, unless secondarily shorter); 106-2. Ribs ?secondarily shortened in association with large palatal vacuities (colosteids and temnospondyls);
107-0. Ribs loosely articulated to arch and intercentrum	107-1. Ribs suturally attached to intercentra and arch (*Panderichthys*); 107-2. Capitulum articulating with posterior margin of centrum (microsaurs, adelogyrinids);
108-0. Ribs with cylindrical shafts	108-1. Ribs much widened so as to overlap one another (*Ichthyostega*);

MEDIAN FINS

109-0. Two distinct dorsal fins	109-1. Dorsal fins lost (*Panderichthys* and all tetrapods);
110-0. Diphycercal caudal fin with *Panderichthys*, modest aspect ratio	110-1. Narrow, pointed caudal fin (*Acanthostega*, and *Ichthyostega*); 110-2. Tail lacks fin and lepidotrichia (all other tetrapods);
111-0. Distinct anal fin	111-1. Anal fin lost (*Panderichthys* and all tetrapods);

APPENDICULAR SKELETON

PECTORAL GIRDLE AND LIMB

112-0. Dermal shoulder girdle connected to operculum and skull roof via post-temporal, supracleithrum and anocleithrum	112-1. Post-temporal and supracleithrum lost, but anocleithrum retained (*Acanthostega*); 112-2. All three bones lost (all tetrapods except *Acanthostega*);
113-0. Interclavicle small	113-1. Interclavicle much enlarged (all early tetrapods);
114-0. Interclavicle oval	114-1. Interclavicle with long posterior stem (*Ichthyostega*, *Acanthostega*, anthracosaurs, seymouriamorphs, diadectomorphs, amniotes, lysorophids); 114-2. Among tetrapods, absence of distinct stem (*Crassigyrinus*, colosteids, temnospondyls, nectrideans, ? microsaurs, adelogyrinids); 114-3. Interclavical lost (aïstopods);
115-0. Cleithrum extends ventrally to midline	115-1. Cleithrum reduced ventrally to expose lateral surface of scapulocoracoid (all tetrapods);
116-0. Cleithrum attached to three processes of scapulocorocoid	116-1. Cleithrum co-ossified with lateral surface of scapular blade (Devonian tetrapods); 116-2. Cleithrum not co-ossified with lateral surface of scapular blade (all post-Devonian tetrapods);
117-0. Postbranchial lamina of cleithrum forming posterior border of opercular chamber	117-1. Loss of postbranchial lamina (all tetrapods except *Acanthostega*);
118-0. Distinct anteroventral process of cleithrum that clasps dorsal process of clavicle	118-1. Loss of anteroventral process of cleithrum (all tetrapods except *Acanthostega*);
119-0. Claviclar stem short and not exposed laterally	119-1. Progressive elongation of stem (all tetrapods); 119-2. Loss of clavicle (aïstopods);
120-0. Scapulocoracoid restricted to glenoid region	120-1. Elaboration of coracoid region but not scapular blade (*Acanthostega* and *Ichthyostega*); 120-2. Elaboration of scapular blade as well as coracoid region (all tetrapods except *Acanthostega* and *Ichthyostega*); 120-3. Loss of scapulocoracoid (adelogyrinids and aïstopods);
121-0. Scapulocoracoid a single center of ossification	121-1. Two centers of ossification (seymouriamorphs); 121-2. Three centers of ossification (amniotes);
122-0. Scapulocoracoid attached to cleithrum by supraglenoid, infra-glenoid, and glenoid buttresses	122-1. Three buttresses converge to form a single surface of attachment, separating foramina (123-125) from cleithrum (*Panderichthys*);

	122-2. Lateral surface of scapulocoracoid expands below cleithrum (all tetrapods);
123-0. Supraglenoid foramen between supraglenoid and glenoid buttresses	123-1. Supraglenoid foramen absent (*Acanthostega*, colosteids, lysorophids);
124-0. Subscapular fossa between supra– and infraglenoid buttresses	124-1. A conspicuous depression on the inner surface of scapulocoracoid (all early tetrapods);
	124-2. Lost of subscapular fossa (lysorophids);
125-0. Supracoracoid foramen between infraglenoid and glenoid buttresses	125-1. One foramen exits through coracoid (most tetrapods);
	125-2. Two foramina (anthracosaurs, seymouriamorphs, amniotes, microsaurs);
126-0. Glenoid canal on medial surface of scapulocoracoid	126-1. Canal absent (anthracosaurs, lysorophids);
127-0. Glenoid pear-shaped faces primarily posteriorly	127-1. Glenoid extends onto coracoid, forming laterally facing articulating surface (all tetrapods);
128-0. Pectoral fin small relative to body	128-1. Forelimb large relative to body (primitive tetrapods);
	128-2. Secondary reduction or limb loss (*Crassigyrinus*, *Westlothiana*, ? nectrideans, lysorophids, adelogyrinids, aïstopods);
129-0. Pectoral fin consisting more half of fin web	129-1. Fin web and lepidotrichia lost (all than tetrapods);
130-0. Limb bones fully ossified in adult individuals with articulating surfaces well-defined	130-1. Reduced ossification resulting in ill-defined articulating surfaces, even in mature individuals (*Crassigyrinus*, lysorophids);
131-0. Humerus an essentially columnar bone, with slightly expanded extremities	131-1. Proximal and distal extremities expanded, but shaft little developed (Devonian genera, *Crassigyrinus*, anthracosaurs, seymouriamorphs, diadectomorphs, colosteids, primitive temnospondyls, nectrideans);
	131-2. Distinct, narrow shaft (*Westlothiana*, amniotes, microsaurs, lysorophids);
	131-3. Humerus lost (adelogyrinids, aïstopods);
132-0. Proximal and distal areas of expansion twisted at 20°	132-1. Torsion 40° (*Crassigyrinus*, *Ichthyostega*);
	132-2. Torsion 25° to 39° (primitive anthracosaurs, colosteids, ? nectrideans, lysorophids);
	132-3. Torsion 45° (seymouriamorphs, primitive temnospondyls);
	132-4. Torsion 80° to 90° (*Westlothiana*, diadectomorphs, amniotes, advanced temnospondyls, microsaurs);
133-0. Proximal articulating surface pear-shaped, no longer than glenoid	133-1. Articulating surface of greater length than glenoid (all tetrapods except Devonian genera);

134-0. Oblique dorsal ridge extending from mid-width of proximal dorsal end of humerus to entepicondylar ridge, enclosing one or more foramina for radial nerves and blood vessels	134-1. Loss of foramina, but retention of ridge (anthracosaurs); 134-2. Loss of ridge and foramina (all tetrapods except Devonian genera, *Crassigyrinus*, and anthracosaurs);
135-0. No deltopectoral crest	135-1. Deltopectoral crest (all tetrapods except Devonian genera);
136-0. Anterior (preaxial) surface of shaft rounded (without anterior keel)	136-1. Anterior keel (Devonian genera, *Crassigyrinus*, anthracosaurs, colosteids, nectrideans); 136-2. Secondary loss of keel (seymouriamorphs, *Westlothiana*, diadectomorphs, amniotes, temnospondyls, microsaurs, lysorophids);
137-0. No supinator process	137-1. Supinator process a part of anterior keel (Devonian genera, anthracosaurs, colosteids); 137-2. Separate supinator process extending from distal end of shaft (seymouriamorphs, *Westlothiana*, diadectomorphs, amniotes, advanced temnospondys, ? nectrideans);
138-0. Ectepicondylar ridge extends distally to overlie area of ulnar articulation	138-1. Ectepicondylar ridge extends obliquely anteriorly to overlie area of radial articulation (all tetrapods except Devonian genera, unless secondarily lost); 138-2. Ectepicondylar ridge lost (lysorophids);
139-0. Postaxial process of humerus extends, as a narrow blade, posterodistally from the posterordistal extremity of the shaft	139-1. Entepicondyle (the tetrapod homologue of the postaxial process) greatly enlarged proximally (all primitive tetrapods); 139-2. As in 139-1, but distal extremity of entepicondyle reduced to parallel entepicondyle (all tetrapods except Devonian genera, anthracosaurs, and seymouriamorphs);
140-0. Entepicondylar foramen pierces shaft along posterior surface and exits at the distal base of the postaxial process	140-1. Entepicondylar foramen penetrates entepicondyle close to its proximal margin (all tetrapods, unless lost); 140-2. Entepicondylar foramen lost (most temnospondyls, lysorophids);
141-0. Distal surface of humerus grooved dorsally, as is the femur, between the distal condyles	141-1. Loss of groove (all tetrapods except *Acanthostega*);
142-0. Presence of a distal process between the postaxial process and the articulating surface for the ulna	142-1. Process greatly reduced (*Ichthyostega*); 142-2. Process lost (all other tetrapods);
143-0. Articulating surfaces for ulna and radius terminal	143-1. Articulating surfaces more ventral than distal (all tetrapods except *Acanthostega*);

144-0. Articulating surface for ulna larger than for radius	144-1. Articulating surface for radius as large or larger than for ulna (all tetrapods);
145-0. Conspicuous ventral diagonal extends from anteroproximal to posterodistal surface of humerus ending at base of postaxial process pierced by numerous foramina	145-1. Ridge absent (all tetrapods except ridge Devonian genera and *Crassigyrinus*);
146-0. Radius, a slender bone significantly longer than humerus or ulna	146-1. Radius shorter than humerus but extending well beyond end of ulna (*Panderichthys*, *Acanthostega*); 146-2. Radius shorter than ulna in which olecranon is ossified (all other early tetrapods); 146-3. Radius lost (adelogyrinids, aïstopods);
147-0. Radius does not articulate with endochondral bone distally	147-1. Radius articulates with radiale and intermedium (? anthracosaurs, seymouriamorphs, diadectomorphs, amniotes, temnospondyls);
148-0. Ulna, a columnar bone widened distally	148-1. Ulna widest proximally (all tetrapods); 148-2. Ulna lost (adelogyrinids, aïstopods);
149-0. Ulna lacks olecranon	149-1. Little development of olecranon (*Acanthostega*); 149-2. Substantial olecranon, unless secondarily reduced (all other tetrapods);
150-0. Ulna with massive distal articulation with ulnare and intermedium	150-1. Broad articulation with ulnare (seymouriamorphs); 150-2. Articulation with intermedium, ulnare, and pisiform (diadectomorphs, amniotes, the microsaur *Pantylus*);
151-0. 4 to 6 elements recognized as homologous with tetrapod carpals	151-1. Carpus largely unossified (*Acanthostega*, primitive anthracosaurs, nectrideans, lysorophids); 151-2. 4 ossified carpals, not including pisiform or distal carpals (seymouriamorphs); 151-3. 7 ossified carpals including pisiform, and three distal carpals, but not centralia (diadectomorphs); 151-4. 11 carpals, including pisiform and two centralia (amniotes); 151-5. 11 carpals, including 4 centralia, but no pisiform (temnospondyls); 151-6. Carpals lost (adelogyrinids, aïstopods);
152-0. Ulnare with large flattened postaxial process	152-1. Small rectangular ulnare, without postaxial process (all tetrapods); 152-2. Huge plate-like ulnare (*Panderichthys*);

153-0. Ulnare articulating with two large carpal elements distally, the more lateral of which articulates with two much smaller elements	153-1. Ulnare articulates with centrale and 4th distal carpal (diadectomorphs); 153-2. Ulnare articulates with centrale and distal carpals 4 and 5 (amniotes);
154-0. Intermedium long and flattened distally between lepidotrichia	154-1. Small rectangular intermedium (all tetrapods);
155-0. No elements recognized as distal carpals, metacarpals, or digits	155-1. Metacarpals and digits unless secondarily lost (all tetrapods);
156-0. Among tetrapods, more than 5 digits in manus (Devonian genera)	156-1. 5 digits in manus (anthracosaurs, seymouriamorphs, diadectomorphs, amniotes, nectrideans); 156-2. 4 digits in manus (colosteids, temnospondyls, microsaurs, lysorophids); 156-3. Loss of digits (adelogyrinids, aïstopods);
157-0. Among tetrapods, phalangeal count of 3, 3, 3, 3, 4, 4, 4, 3	157-1. Phalangeal count of 2, 3, 4, 5, 3 (anthracosaurs, seymouriamorphs, diadectomorphs, *Acanthostega*, amniotes); 157-2. Phalangeal count of 2, 2, 3, 3 (colosteids, temnospondyls); 157-3. Phalangeal count of 2, 3 ?, 4, 3, 2 (nectrideans); 157-4. Phalangeal count of 2, 3, 3, 2+ (microsaurs); 157-5. Phalangeal count of 3, 3 ?, 3, 2 (lysorophids);

PELVIC GIRDLE AND LIMB

158-0. Pelvic girdle a single paired element	158-1. Pelvic girdle consisting of three areas of ossifications, pubis, ischium, and ilium (all tetrapods unless secondarily reduced); 158-2. Pelvic girdle lost (adelogyrinids, aïstopods);
159-0. Pelvic girdle not attached to vertebral column	159-1. Pelvic girdle attached to the vertebral column via one or more pairs of sacral ribs (all tetrapods with limbs);
160-0. Pelvic girdle not attached at the ventral midline	160-1. Halves of girdle joined ventrally via the puboischiadic symphysis (all tetrapods);
161-0. Acetabulum facing posteriorly	161-1. Acetabulum facing laterally (all tetrapods with limbs);
162-0. Iliac ramus of pelvis short without blade attached to sacral ribs	162-1. Iliac blade with short dorsal and longer posterior process (*Acanthostega*, *Ichthyostega*, anthracosaurs); 162-2. Bifurcate iliac blade with larger dorsal but shorter posterior process (*Crassigyrinus*, seymouriamorphs, microsaurs); 162-3. Reduced dorsal process extending from the margin of posteriorly directed blade (*Westlothiana*, diadectomorphs, amniotes);

	162-4. Non-bifurcate iliac blade, extending dorsally and somewhat posteriorly (colosteids, temnospondyls, nectrideans, lysorophids);
163-0. No openings in area of pubis	163-1. Two obturator foramina (*Ichthyostega*, anthracosaurs);
	163-2. One obturator foramen (all other tetrapods);
164-0. No ossification in area of ischium	164-1. Ischium a neomorph (all tetrapods);
	164-2. Ischium not ossified (adelogyrinids, aïstopods);
165-0. Femur, a short columnar bone with little development of ventral ridge system	165-1. Femur more elongate, with well-developed ventral ridge system, including internal trochanter and adductor crest (all tetrapods unless secondarily lost);
	165-2. Adductor crest absent, intertrochanteric fossa ill-defined (*Crassigyrinus*);
	165-3. Femur lost (adelogyrinids, aïstopods);
166-0. Distal articulating surfaces narrow and terminal	166-1. Distal articulating surfaces broader and facing ventrally as well as distally (all tetrapods);
167-0. Tibia much longer than femur	167-1. Tibia shorter than femur (all early tetrapods);
	167-2. Tibia lost (adelogyrinids, aïstopods);
168-0. Tibia flattened distally between lepidotrichia	168-1. Articulating facets for tarsals (all tetrapods);
169-0. Fibula with large, flattened postaxial process	169-1. Loss of postaxial process (all tetrapods);
	169-2. Fibula lost (adelogyrinids, aïstopods);
170-0. Shaft of fibula stout and much shorter than tibia	170-1. Shaft slightly shorter than tibia (Devonian tetrapods, nectrideans);
	170-2. Fibula longer than tibia (all other early tetrapods);
171-0. Proximal articulating surface with femur larger than that of tibia	171-1. Area of proximal articulation with femur small than that of tibia (all tetrapods);
172-0. Fibula articulating distally with elongate, flattened fibulare and intermedium	172-0. Fibulare and intermedium shorter, polygonal elements (all tetrapods unless lost);
	172-1. Tarsals unossified (adelogyirnids, aïstopods);
173-0. Intermedium does not articulate distally with endochondral elements	173-1. Intermedium articulates with two more distal tarsals (all known primitive tetrapods except where limbs are reduced);
	173-2. Intermedium integrated into astragalus (amniotes, some microsaurs);
174-0. Fibulare elongate, with postaxial process	174-1. Short, without postaxial process (primitive tetrapods);
175-0. Fibulare articulates with three elongate elements	175-1. Fibulare articulates with three distal tarsals (*Ichthyostega*);

	175-2. Fibulare articulates with distal tarsals 4 and 5 (other early tetrapods);
176-0. No tarsal recognized distal to tibia	176-1. Tibiale and intermedium distal to tibiato (seymouriamorphs, microsaurs, lysorophids);
	176-2. Tibiale, intermedium, and centrale distal to tibia (anthracosaurs, ? *Westlothiana*, diadectomorphs, colosteids, temnospondyls);
	176-3. Area of tibiale incorporated with intermedium and proximal centrale, to form astragalus (amniotes, some microsaurs);
177-0. No elements recognized as centralia	177-1. One centrale (*Ichthyostega*);
	177-2. Two centralia (amniotes);
	177-3. Three centralia (microsaurs);
	177-4. Four centralia (anthracosaurs, ? *Westlothiana*, colosteids, temnospondyls);
178-0. No elements recognizable as distal tarsals, metatarsals, or digits	178-1. Metatarsals and digits unless secondarily lost (all tetrapods);
179-0. Among tetrapods, more than 5 digits in pes (*Ichthyostega*)	179-1. 5 digits (all other early tetrapods unless lost);
	179-2. Digits of pes lost (adelogyrinids, aïstopods);
180-0. Among tetrapods, phalangeal count of 3, 4, 2, 3, 4, 4, 3 (*Ichthyostega*)	180-1. 2, 3, 4, 5, 5 (anthracosaurs);
	180-2. 2, 3, 4, 5, 4 (seymouriamorphs, *Westlothiana*, diadectomorphs, amniotes);
	180-3. 2, 2, 3, 4, 3 (colosteids, temnospondyls);
	180-4. 2, 3, 4, 4, 2? (nectrideans);
	180-5. 2, 3, 4, 5, 3 (microsaurs);
	180-6. 2, 3, 3, 3, 2 (lysorophids);
	SCALES
181-0. Large, uniform cycloid scales covering all of trunk	181-1. Clear distinction between dorsal and ventral scales (all early tetrapods);
182-0 Dorsal scales present	182-1. Dorsal scales absent (*Crassigyrinus*, anthracosaurs, diadectomorphs, amniotes, nectrideans, lysorophids);
	182-2. Pebbly dorsal ossicles (aïstopods);
183-0. Enlarged scales (basal scutes) on each side of the bases of all median and paired fins (except caudal)	183-0. Loss of basal scutes (*Panderichthys*, all tetrapods);
184-0. Lepidotrichia cover distal ends of fins	184-0. Lepidotrichia lost (all tetrapods except caudal region of *Acanthostega, Ichthyostega*).

APPENDIX II DATA MATRIX

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Node                      12345678901234567890123456789012345678901234567890123456789
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Ichthyostega              11300121010100?20001001000110001100010001100000001?021???0?1
Crassigyrinus             11001201110200230001000 0?0011000100000101100000011021 1?100?
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Westlothiana              1151?241000400?41111101100011200 0?11112011?1000011?21111?03
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Amniotes                  1151?241020400341111101100011200011111221111002011221111105
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Nectrideans               10611251000600441111?01100011200011111201110000011021111008
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Adelogyrinids             11801241040500541111001231011200011111201 1?100021102111100a
Lysorophids               1191?25203261064111??11201011200011111201122110211421111 01b
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Ichthyostega              00000130000011?????????10?????????12?20?0201?01011112111111
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Seymouriamorphs           41100131112011110211?12121001100201312000221101001212111211
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Diadectomorphs            61111131113011 11??1111?13100110121141201022120100121211121 1
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Colosteids                40100131013011110111111121000100001302000200102001212121211
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Microsaurs                41100131115011 11?01111215311110020131201 1?211010012121?1211
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Lysorophids               41123131116111110011212153111102200 3?2011322101001212111211
Aistopods                 2111?131113011110011212112101212211512012322311001212131211
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Seymouriamorphs         12120120111013121221111211121121 21?111111112211111121111?1?
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Adelogyrinids           13?2?????21?3??????????????3?2??6???13?2?????23?2?2??2?????
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Aïstopods               23?2?????21?3??????????????3?2??6???13?2?????23?2?2??2?????
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Loxommatids             ???????
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Amniotes                1121111
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Nectrideans             1141111
Microsaurs              1151011
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Lysorophids             1161111
Aïstopods               12?1211
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Revised Upper Silurian-Lower Devonian ichthyostratigraphy of northern France and southern Belgium (Artois-Ardenne)

by Alain BLIECK, Daniel GOUJET, Philippe JANVIER, and Francis MEILLIEZ
(Contribution to IGCP Project 328 "Palaeozoic Microvertebrates")

Abstract. — 39 localities within the Upper Silurian-Lower Devonian sequence of the Ardenne-Artois area yield vertebrate species which allow correlation with at least the vertebrate succession of the Welsh Borderland, England, and of Spitsbergen. Invertebrate fossils and palynomorphs suggest a correlation with the marine facies elsewhere in Europe. Relating the vertebrate biostratigraphy to that of conodont-graptolite-dacryoconarids is problematic but the postulated acme of the local vertebrate faunas in the lower *crouchi* zone of Artois may be related to the high sea level of the *eurekaensis* zone, and the impoverishment of the upper *leachi* and lower *dunensis* zones to the low sea level of the upper Lochkovian-Pragian.

Keywords. — Upper Silurian, Lower Devonian, vertebrates, northern France (Artois), southern Belgium (Ardenne), biostratigraphy, correlation.

Révision de l'ichthyostratigraphie du Silurien supérieur-Dévonien inférieur du nord de la France et du sud de la Belgique (Artois-Ardenne)

Résumé. — Le Silurien supérieur-Dévonien inférieur de la région Ardenne-Artois a livré 39 localités fossilifères à Vertébrés que l'on peut corréler au moins aux séquences à Vertébrés de la Bordure Galloise (Angleterre) et du Spitsberg. Les invertébrés et palynomorphes présents autorisent des corrélations avec les faciès marins, ailleurs en Europe. La mise en relation de l'échelle biostratigraphique fondée sur les Vertébrés avec celle qui est fondée sur les Conodontes-Graptolites-Dacryoconarides n'est pas résolue. Cependant l'acmé des faunes de Vertébrés dans la partie inférieure de la zone à *crouchi* en Artois pourrait être liée au haut niveau marin de la zone à *eurekaensis*. A l'inverse, l'appauvrissement des faunes des zones à *leachi* supérieure et à *dunensis* inférieure serait lié au bas niveau marin du Lochkovien supérieur-Praguien.

Mots-clés. — Silurien supérieur, Dévonien inférieur, Vertébrés, nord de la France (Artois), sud de la Belgique (Ardenne), biostratigraphie, corrélation.

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INTRODUCTION

This paper purposes to make available the results previously published in French on the Upper Silurian-Lower Devonian ichthyofaunas of northern France and southern Belgium. The most recent results have been presented in two papers by BLIECK & JANVIER (1989) and BLIECK & GOUJET (1991), wherein older works are referred to and listed. We also deal with a biostrati-

graphical synthesis on the upper Pridoli to Emsian ichthyofaunas of the region, following the tentative synthesis published thirteen years ago by one of us (BLIECK, 1982a). This ichthyostratigraphical scale is correlated with the spore-zonations of the Lower Old Red Sandstone (ORS) facies from Britain and Germany, which have been themselves correlated with the standard Lochkovian-Pragian sequence of Bohemia (STREEL *et al.*, 1987). At the end of the paper, a discussion is also initiated about correlations with event-stratigraphy and eustatic curves for Lower Devonian times.

GEOLOGICAL SETTING

Between the Channel and the Rhine river most Palaeozoic rocks crop out within the Ardenne area, southeast of the Sambre and Meuse rivers (Fig. 1). North of them, within the Brabant area, isolated small outcrops occur along valleys, below an unconformable Upper Cretaceous to Eocene cover. West of the Ardenne, below the Upper Cretaceous cover, tiny outcrops are aligned along the Artois hilly ridge as far as the Boulonnais. Examination of all these outcrops reveals intermittent and differentiated tectonic activity since the end of Cretaceous time.

All these Palaeozoic rocks include Devonian sediments that were deposited along the southern margin of the Old Red Sandstone Continent as a Variscan cover that rests unconformably above a strongly folded Caledonian substratum, Lower Palaeozoic in age. Later on, the Carboniferous Variscan shortening has differentiated two major structural domains, the northern Brabant Parautochthon and the southern Ardenne Allochthon. These domains are separated by a complex faulted zone which is not the only one within the Allochthon. Thus the Ardenne Allochthon appears as a stack of large tectonic sheets dipping gently to the SSE rather than a single huge nappe, the so-called Dinant Nappe (see discussion *in* MEILLIEZ & MANSY, 1990). The bulk Variscan shortening is estimated at 40% but this is not uniformly distributed; it is higher across each thrust zone and roughly increases by adding effects southwards.

Between the Rhine river and the Liévin area (Fig. 1 and locality 4, Fig. 2), the frontal faulted zone is made of anastomosing flat-lying thrusts, together with the overlying Ardenne Allochthon and the underlying Brabant Parautochthon. The well-known Midi Overthrust is one of these faults. Such a structure is documented from deep seismic data and boreholes (see review *in* RAOULT, 1988). Between the Liévin area and the Channel, the frontal faulted zone is made of steeply dipping faults that are difficult to discriminate from those the Cenozoic tectonics has reactivated. Only some of these faults were mapped during coal mining (which stopped in December 1990). The actual link with the Boulonnais inlier is still debated (Bl on Fig. 1).

The Ardenne Allochthon and the Brabant Parautochthon both encompass a Devono-Carboniferous Variscan cover unconformably overlying a Lower Palaeozoic substratum. Within the Brabant Massif, the Variscan cover is unfolded and forms adjacent monoclines. Within the former, the cover wraps around antiformal stacks with substratum inliers as a core. Similar are the Rocroi, Serpont and Stavelot massifs that determine a saddle separating the southern Neufchâteau synclinorium from the northern Dinant synclinorium. Linear inliers lie along the frontal thrust zone between Charleroi and Liège on the east (Condroz antiformal stack BC on Fig. 1) and in the Liévin area on the west (Lv).

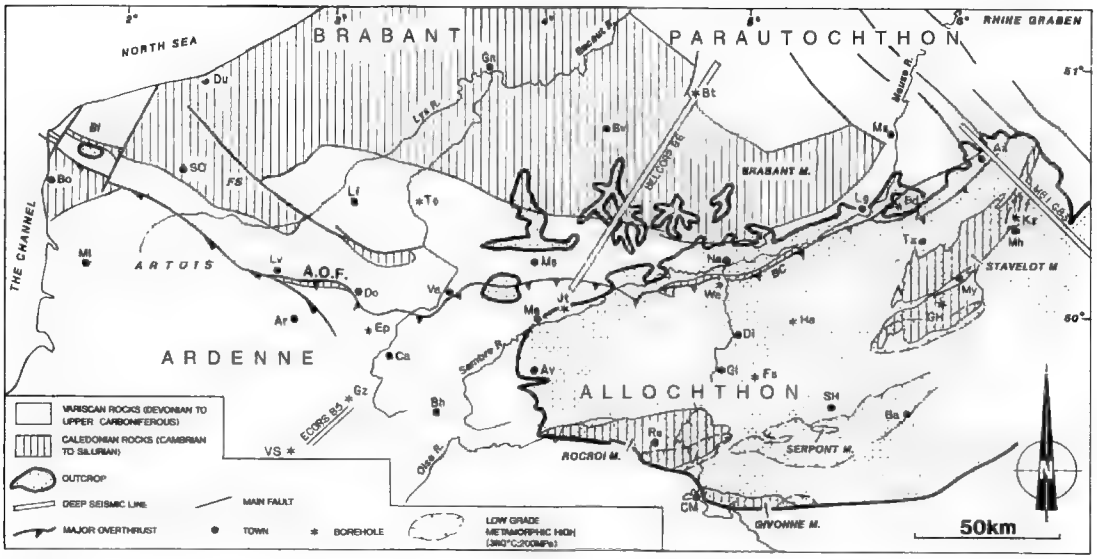


FIG. 1 — Simplified geological map between the Channel and the Rhine river. The Variscan shortening has differentiated two major structural domains that are separated by a complex gently south dipping thrust zone (A.O.F.: Ardenne Overthrust Front). The Midi Overthrust is one of these thrusts. Each of the two major domains encompasses a Lower Palaeozoic sedimentary basement and a Devono-Dinantian sedimentary cover. The basement was deformed and subsequently eroded, giving rise to the Caledonian unconformity. Basement can be observed through the Brabant and Flandre-sud (PS) horst-like relicts within the Variscan Parautochthon, and through the Rocroi, Stavelot, Serpont, Givonne, Condroz Strip (BC), Artois and Boulonnais (Bl) inliers within the Variscan Allochthon. The name "synclinorium de Namur" has to be discarded as it brackets various structural domains below the Coal Basin.

Boreholes: Bt- Boischoot, Bd- Bolland, Ep- Epinoy, Fo- Focant, GH- Grand Halleux, Gz- Gouzeaucourt, Ha- Havelange, Jt- Jeumont, Kz- Konzen, To- Tournai, VS- Vermandovilliers, We- Wépion.

Localities: Aa- Aachen, Ar- Arras, Av- Avesnes-s/Helpe, Ba- Bastogne, Bh- Bohain, Bo- Boulogne-s/Mer, Bx- Bruxelles, Ca- Cambrai, CM- Charleville-Mézières, Di- Dinant, Do- Douai, Du- Dunkerque, Gn- Gent, Gi- Givet, Lg- Liège, Li- Lille, Lv- Liévin, Ma- Maubeuge, Mh- Monschau, Mo- Mons, Ms- Maastricht, Mt- Montreuil, My- Malmédy, Na- Namur, Ro- Rocroi, SH- Saint-Hubert, SO- Saint-Omer, Tx- Theux, Va- Valenciennes.

Carte géologique simplifiée entre la Manche et le Rhin. Le raccourcissement varisque a différencié deux domaines structuraux majeurs séparés par une zone complexe de chevauchements à pendage sud faible (A.O.F.: chevauchement frontal ardennais). La Faille du Midi est l'un de ces chevauchements. Chacun de ces deux domaines majeurs comporte un socle sédimentaire du Paléozoïque inférieur et une couverture sédimentaire dévono-dinantienne. Le socle a été déformé puis érodé donnant naissance à la discordance calédonienne. Ce socle peut être observé à la faveur de reliques en horst sur le Brabant et la Flandre méridionale (PS) dans le Parautochtone Varisque, ainsi qu'à la faveur des massifs de Rocroi, Stavelot, Serpont, Givonne, de la Bande du Condroz (BC), des petits affleurements d'Artois et du massif de Ferques dans le Boulonnais (Bl) dans l'Allochtone Varisque. Le terme de « synclinorium de Namur » doit être abandonné puisqu'il recouvre des domaines structuraux variés sous le Bassin Houiller.

Forages : Bt- Boischoot, Bd- Bolland, Ep- Epinoy, Fo- Focant, GH- Grand Halleux, Gz- Gouzeaucourt, Ha- Havelange, Jt- Jeumont, Kz- Konzen, To- Tournai, VS- Vermandovilliers, We- Wépion

Localités : Aa- Aachen, Ar- Arras, Av- Avesnes-s/Helpe, Ba- Bastogne, Bh- Bohain, Bo- Boulogne-s/Mer, Bx- Bruxelles, Ca- Cambrai, CM- Charleville-Mézières, Di- Dinant, Do- Douai, Du- Dunkerque, Gn- Gent, Gi- Givet, Lg- Liège, Li- Lille, Lv- Liévin, Ma- Maubeuge, Mh- Monschau, Mo- Mons, Ms- Maastricht, Mt- Montreuil, My- Malmédy, Na- Namur, Ro- Rocroi, SH- Saint-Hubert, SO- Saint-Omer, Tx- Theux, Va- Valenciennes.

It has been suggested (MEILLIEZ *et al.*, 1992) that within the Brabant Parautochthon, the main WNW-ESE trend and its subsidiary SW-NE trend reflect the Upper Silurian (?) to Devonian structural frame of the southern margin of the Old Red Sandstone Continent. This margin accomodated a synsedimentary extension. The bulk southward thickening of the early deposits and

the bulk northward migration of the transgressive frontal line are in agreement with the image of a tilted-blocks puzzle. The earliest and strongest induced subsidence occurs south of most of the substratum inliers. Thus the Upper Silurian to Lower Devonian transition is likely to occur under marine conditions SE of the Rocroi massif, in Liévin area, and probably SE of the Stavelot massif (see review *in* MEILLIEZ *et al.*, 1992). Due to the same effect is the presence of Lower Devonian with acritarchs at the bottom of an early graben in the Brabant Parautochthon (VANGUESTAINE *et al.*, 1989).

All the fossiliferous localities studied here belong to the Ardenne Allochthon, on either side of the Dinant synclinorium (Fig. 2): 1-17 along the northern fringe and 24-25, 36, 37? along the southern fringe; 26-33, 35 in the Neufchâteau synclinorium; 18-23, 34 north of the Stavelot massif.

THE SEQUENCE OF ARTOIS

Figure 3 is a summary of all vertebrate taxa collected from shafts, boreholes and outcrops on the northern edge of the Dinant western concealed synclinorium. It is a synthesis of the whole fauna, including the corrected data of BLIECK & JANVIER (1989, Figs. 3 and 11 in which printing mistakes occurred, particularly concerning the location of the *Pteraspis rostrata* biozone). We find in Artois the biozones defined by E. I. WHITE in the Lower ORS of the Welsh Borderland; this zonation was the first such based on fishes, and the first biozonation in the Lower ORS (references *in* STUBBLEFIELD, 1985). The *Protopteraspis* and *Rhinopteraspis crouchi* zones were found in Liévin shaft No 6 (GOUJET & BLIECK, 1979), and the *Pteraspis rostrata* zone in between at shaft Vimy 1bis (BLIECK & JANVIER, 1989), the *Althaspis* zone having been defined above the *R. crouchi* zone (see WHITE, 1956). The Silurian/Devonian boundary has been precisely identified at Vimy 1bis upon the appearance of the chitinozoan *Eisenackitina bohemica* (at about – 752 m: RACHEBOEUF ed., 1986, Figs. 12-13); and at Noulette upon the appearance of the brachiopod *Mesodouvillina (M.) triculta* (at about –850m, *ibid.*, in cenozone III).

Above this subsurface sequence, the outcropping Matringhem Sandstones correspond to the AB and/or Su spore-zones *sensu* STEEMANS (1989, Pernelle section and Jaeger quarry, Fig. 84 and 107), based on the occurrence of *Apiculiretusispora plicata*, *Dictyotriletes subgranifer* and *Emphanisporites rotatus* as determined by STREEL (*in* LECLERCQ, 1975, localities No 24 and 37; loc. 24 being very near the *Rhinopteraspis dunensis* locality of Vincly: BLIECK & JANVIER, 1989). The Matringhem Sandstones are thus dated as upper Pragian-lower Emsian.

It must be mentioned here that, at the base of the sequence, the *Traquairaspis* zone should be renamed, following the advice of HEDBERG (1979, p. 88). This zone is indeed defined after two species of heterostracans collected first in the Welsh Borderland. These species have been recently revised by TARRANT (1991) under *Phialaspis symondsi* and *Toombsaspis pococki;* so TARRANT renames the *Traquairaspis* zone, the *Phialaspis symondsi-Toombsaspis pococki* zone (*ibid.*, p. 402). However it seems to one of us (A. B.) that both species have to be kept in a single genus, *Phialaspis*, as originally made by WHITE (1946). So the *Traquairaspis* zone has to be simply renamed *Phialaspis* zone (Figs. 3 and 5). Nevertheless none of the *Phialaspis* species has been found in Artois where the *Phialaspis* zone is identified on other taxa (the

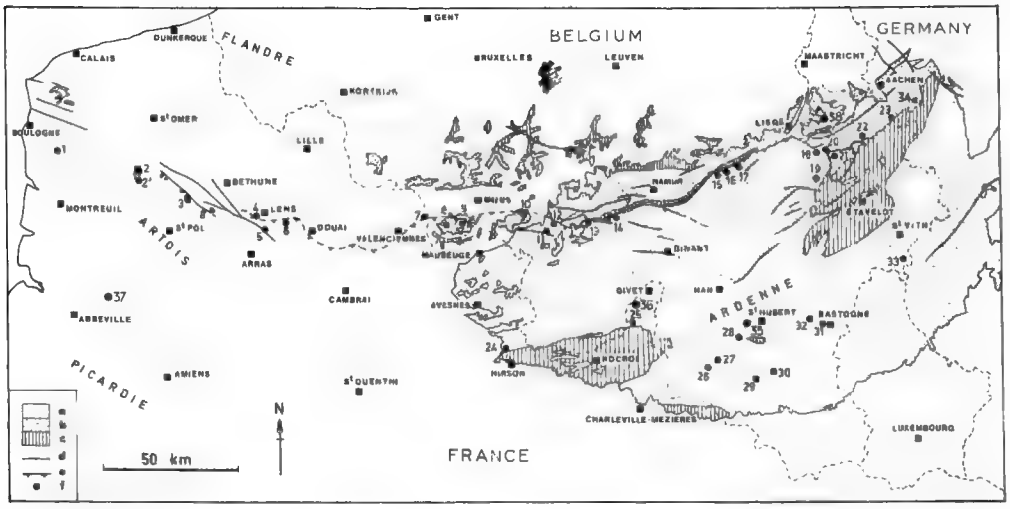


FIG. 2. — Lower Devonian localities of northern France and southern Belgium, with heterostracans and other lower vertebrates, after BLIECK (1982a, Fig.1 completed), BLIECK & JANVIER (1989), BLIECK & GOUJET (1991).
a- Post-Palaeozoic, b- Upper Palaeozoic (Devonian-Carboniferous), c- Lower Palaeozoic (Cambrian-Silurian), d- faults, e- Midi Overthrust, f- fossiliferous localities.
1- Samer. 2- Dennebreucq. 2'- Vincly, 3- Pernes-en-Artois, 4- Liévin, 5- Vimy. 6- Beaumont-en-Artois, 7- Quiévrechain, 8- Wihéries, 9- Bois de Colfontaine. 10- Binche. 11- Thuin, 12- Landelies. 13- Acoz. 14- Vitrival. 15- Ben Ahin. 16- Huy. 17- Ombret, 18- Fraipont, 19- Nonceveux 20- Pepinster. 21- Fays, 22- Étang de la Gileppe, 23- Étang d'Eupen. 24- Mondrepuis, 25- Moulin de Fétrogne. 26- Carlsbourg, 27- Paliseul, 28- Glaireuse (= Villance). 29- Bois d'Autrouge (= Rossart), 30- La Mouline, 31- Bastogne, 32- Mandé Saint-Étienne, 33- Saint-Vith, 34- Hautes Fagnes (Hohes Venn. Zweifall, Solchbach, etc.), 35- Arville. 36- Vireux. 37- Coulonvillers. 38- Bolland.

Localités d'âge Dévonien inférieur du nord de la France et du sud de la Belgique, ayant livré des Hétérostracés et d'autres Vertébrés, d'après BLIECK (1982a, Fig. 1, complétée), BLIECK & JANVIER (1989), BLIECK & GOUJET (1991).
a- post-Paléozoïque, b- Paléozoïque supérieur (Dévonien-Carbonifère), c- Paléozoïque inférieur (Cambrien-Silurien), d- failles, e- Faille du Midi, f- localités fossilifères.
1- Samer, 2- Dennebreucq, 2'- Vincly, 3- Pernes-en-Artois, 4- Liévin, 5- Vimy, 6- Beaumont-en-Artois, 7- Quiévrechain, 8- Wihéries, 9- Bois de Colfontaine, 10- Binche, 11- Thuin, 12- Landelies, 13- Acoz, 14- Vitrival, 15- Ben Ahin, 16- Huy, 17- Ombret, 18- Fraipont, 19- Nonceveux, 20- Pepinster, 21- Fays, 22- Étang de la Gileppe, 23- Étang d'Eupen, 24- Mondrepuis, 25- Moulin de Fétrogne, 26- Carlsbourg, 27- Paliseul, 28- Glaireuse (= Villance), 29- Bois d'Autrouge (= Rossart), 30- La Mouline, 31- Bastogne, 32- Mandé Saint-Étienne, 33- Saint-Vith, 34- Hautes Fagnes (Hohes Venn: Zweifall, Solchbach, etc.), 35- Arville, 36- Vireux, 37- Coulonvillers, 38- Bolland.

thelodonts *Turinia pagei* and *Tu.* sp. A which, in the Welsh Borderland, are known in the "*Traquairaspis* zone": BLIECK & GOUJET, 1986).

A main difference appears when compared to the Welsh Borderland sequence: the Liévin Group of Artois has been fully cored and we know exactly the respective stratigraphical location of all the fossiliferous horizons. No overlap of the different vertebrate index-species is indicated, contrary to what is assumed in the Ardenne massif from the spore analysis (STEEMANS, 1989; STREEL *et al.*, 1987). This is one of the reasons why we could define a *Pteraspis rostrata* zone in Vimy shaft No 1 bis (BLIECK & JANVIER, 1989).

When counting all the vertebrate species through the stratigraphical log (Fig. 3), the richest horizon is found at Liévin shaft No 6, within the lower Pernes Formation (the so-called Pernes

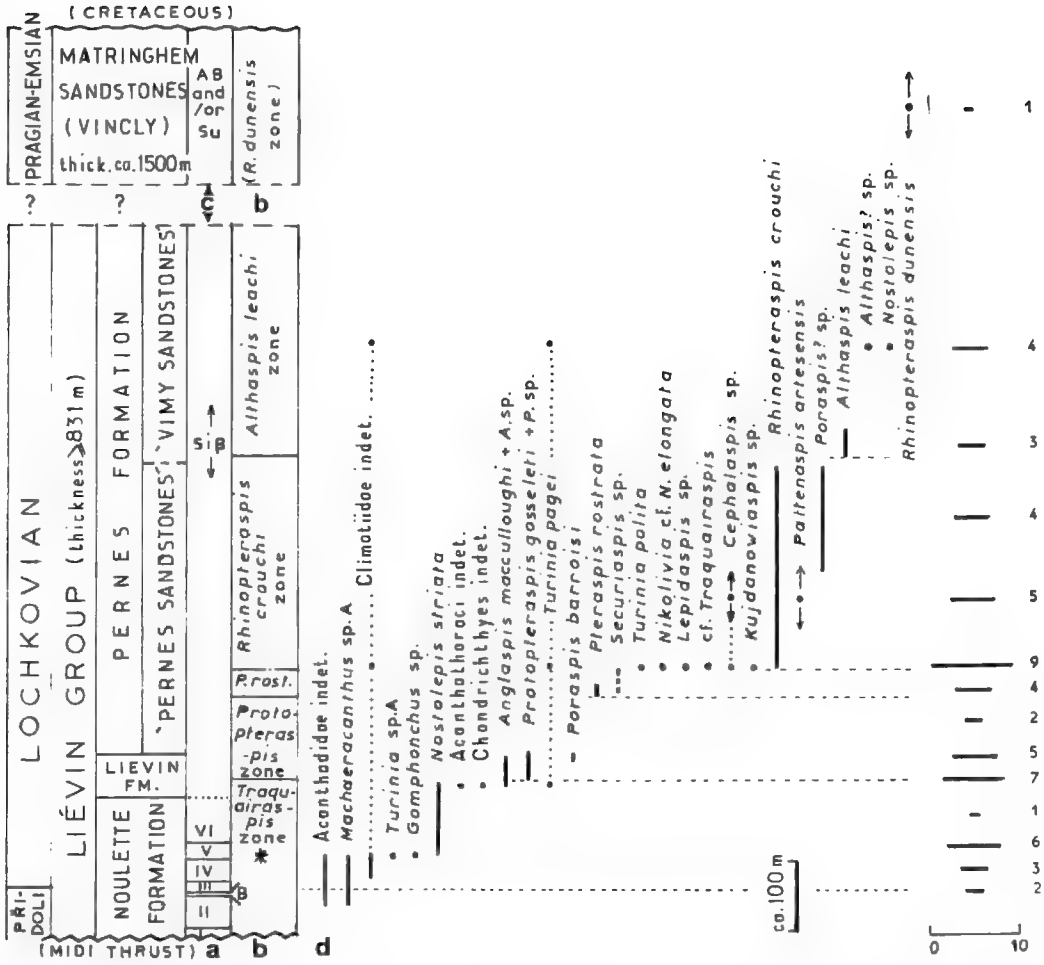


FIG. 3. — Synthetic stratigraphy of the uppermost Silurian-Lower Devonian sequence of Artois (Pas-de-Calais, France); chrono- and lithostratigraphy after RACHEBŒUF ed. (1986), LECLERCQ (1975). a, invertebrate-based assemblage biozones (cenozones) I-VI of RACHEBŒUF ed. (1986), with B, the bryozoan-bearing beds. b, vertebrate-based interval biozones (ichthyozones) of BLIECK & JANVIER (1989). c, spore zones after STEEMANS (1989; modified according to BLIECK & GOUJET, 1991) and STREEL *in* LECLERCQ (1975). d, vertebrate species after GOUJET & BLIECK (1979), BLIECK & GOUJET (1986), BLIECK & JANVIER (1989). The right column gives the number of species of each assemblage.

Abbr.: *P. rost.* = *Pteraspis rostrata* zone.

* *Traquairaspis* zone: this biozone should be renamed *Phialaspis* zone (= *Phialaspis symondsi-Toombsaspis pococki* zone of TARRANT, 1991; *Toombsaspis* being considered here a synonym of *Phialaspis*).

Synthèse stratigraphique du Silurien terminal-Dévonien inférieur d'Artois (Pas-de-Calais, France) : chrono- et lithostratigraphie d'après RACHEBŒUF éd. (1986), LECLERCQ (1975). a, biozones d'assemblages d'invertébrés (cénozones) I à VI de RACHEBŒUF éd. (1986) avec les bancs à Bryozoaires (B). b, biozones d'intervalle de Vertébrés (ichthyozones) de BLIECK & JANVIER (1989). c, biozones de spores d'après STEEMANS (1989 ; modifié selon BLIECK & GOUJET (1991) et STREEL in LECLERCQ (1975). d, espèces de Vertébrés d'après GOUJET & BLIECK (1979), BLIECK & GOUJET (1986), BLIECK & JANVIER (1989). La colonne de droite donne le nombre d'espèces pour chaque assemblage.

Abrév. : P. rost. = *zone à* Pteraspis rostrata.

* *Zone à* Traquairaspis : *cette biozone devrait être rebaptisée zone à* Phialaspis (= *zone à* Phialaspis symondsi-Toombsaspis pococki *de Tarrant, 1991 ;* Toombsaspis *étant considéré ici comme synonyme de* Phialaspis).

Sandstones, also known in outcrops at the Pernes quarries), at the base of the *R. crouchi* zone. Nine taxa have been collected here but we can add a tenth one, viz., Pteraspididae gen. et sp. indet. GOUJET & BLIECK (1979, Fig. 3 D-F and Pl. XXIII: 8), partly based on fragmentary cornual plates (*ibid.*, Fig. 3 D-E) which look like those of both *Parapteraspis jackana* and *Larnovaspis stensioei* (*sensu* BLIECK, 1984). Above and below this horizon, the ichthyofauna is much poorer, probably because of both scarce outcrops and taphonomical conditions. It can however be noted that this *R. crouchi* assemblage (reconstructed by BLIECK & JANVIER, 1989, Fig. 12) is correlated to the part of the Ben Nevis Formation of Spitsbergen where we find the *Protopteraspis vogti* horizon (GOUJET & BLIECK, 1977), which is also the richest horizon of the Lochkovian sequence of Spitsbergen (BLIECK *et al.*, 1987, Fig. 2; 30 different genera). This time span thus seems to correspond to an acme of the ichthyofaunas on both sides of Laureuropa.

THE SEQUENCE OF ARDENNE

In contrast to the Artois sequence, the Ardenne one is not continuous. It is compiled from isolated, outcropping fossil localities, which have been correlated to both the British and the Artois sequences. Some are linked to the spore zones of STEEMANS (1989), some are not (Fig. 4). Generally speaking, there is a rather good agreement between the different scales, and we find in Ardenne the *crouchi-leachi-dunensis* succession already defined in the Welsh Borderland.

However a problem arises:

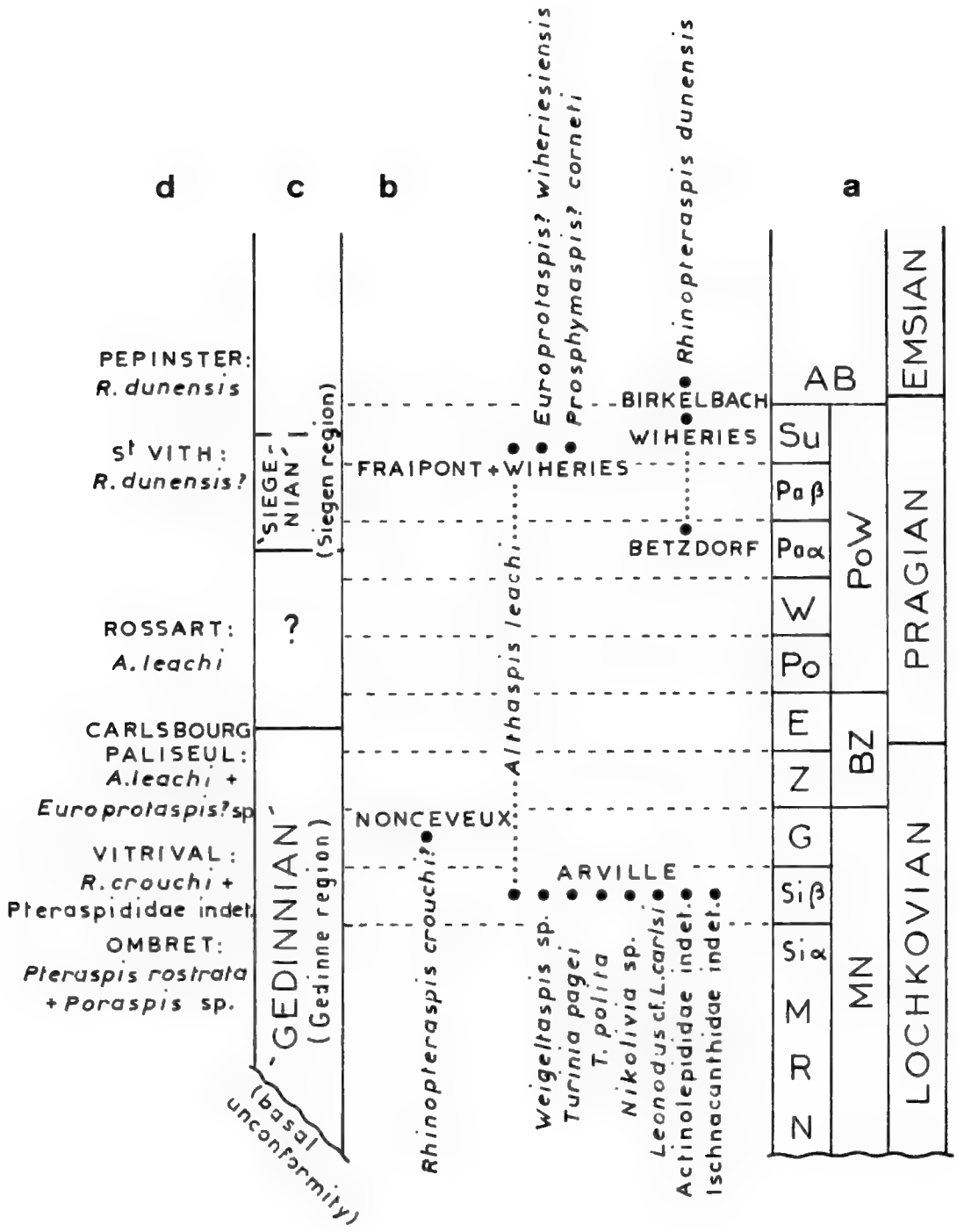
a) Arville (loc. 35, Fig. 2), which bears an *Althaspis leachi* assemblage and is thus considered stratigraphically younger than Nonceveux with its *R. crouchi?* specimens (BLIECK & GOUJET, 1991), has been correlated by STEEMANS (1989: *in* STREEL *et al.*, 1987) to an older spore zone than Nonceveux (Fig. 4);

b) Betzdorf in the Siegen area of western Germany (= Betzdorf-Kirchen *in* BLIECK & JAHNKE, 1980), yielded *Rhinopteraspis dunensis* and should be considered younger than Wihéries or Fraipont (loc. 8, 18, Fig. 2) which yielded *A. leachi*; but Betzdorf is correlated by STEEMANS (1989) to an older spore zone (Fig. 4).

These results led STEEMANS to propose stratigraphical overlaps between the different pteraspid index-species *crouchi-leachi-dunensis* (Fig. 4). The main contradiction to this scheme is that no locality with *crouchi* + *leachi* or *leachi* + *dunensis* has ever been found. We thus hypothesized reworked thanatocenoses in the Ardenne spore assemblages, which was denied by STEEMANS (*in* BLIECK & GOUJET, 1991). The problem remains thus unresolved.

By means of correlation with the chitinozoan succession of Brittany (France) and Bohemia (Czech Republic), the spore zonation is linked to the Lochkovian-Pragian type series (STREEL *et al.*, 1987). The Lochkovian/Pragian boundary falls within the *leachi* distribution interval. Futhermore there is no definition of the "Gedinnian/Siegenian" boundary, neither in the type Gedinne area of Belgium, nor in the type Siegen area of Germany.

A probable *Pteraspis rostrata* zone also occurs in the Ardenne massif at Ombret (loc. 17, Fig. 2) but is not correlated to any part of the spore scale.


d
c
b
a
PEPINSTER:
R. dunensis
st VITH:
R. dunensis?
ROSSART:
A. leachi
CARLSBOURG
PALISEUL:
A. leachi +
Europrotaspis? sp
VITRIVAL:
R. crouchi +
Pteraspididae indet.
OMBRET:
Pteraspis rostrata
+ Poraspis sp.
SIEGENIAN
(Siegen region)
?
GEDINNIAN
(Gedinne region)
(basal unconformity)
FRAIPONT + WIHERIES
NONCEVEUX
ARVILLE
BIRKELBACH
WIHERIES
BETZDORF
Rhinopteraspis crouchi?
Althaspis leachi
Weigeltaspis sp.
Turinia pagei
T. polita
Nikolivia sp.
Leonodus cf. L. carlsi
Actinolepididae indet.
Ischnacanthidae indet.
Europrotaspis? wiheriesiensis
Prosphymaspis? corneli
Rhinopteraspis dunensis
AB
Su
Paβ
Paα
W
Po
E
Z
G
Siβ
Siα
M
R
N
PoW
BZ
MN
EMSIAN
PRAGIAN
LOCHKOVIAN

The richest assemblage was collected in Arville and correlated to part of the succession of northern Spain (BLIECK & GOUJET, 1991) because of the occurrence of the chondrichthyan *Leonodus* MADER (1986; see also WANG, 1993).

INTERREGIONAL CORRELATION AND CONCLUSION

Six ichthyozones have been defined from the base of the Devonian up to the lower Emsian; they have been originally documented in the Welsh Borderland of England, and then complemented in Artois, Ardenne and part of the Rhenish Slate Massif (Fig. 5). All the ichthyozones are interval biozones, defined at their base on the first occurrence of their index-species. Due to the scarcity of outcrops in these green, wet Atlantic provinces of western Europe, and to the taphonomic conditions in several kilometers thick, detrital series (the Lower Old Red Sandstone), the fossiliferous record is not good and the precision of the ichthyozones is not very high.

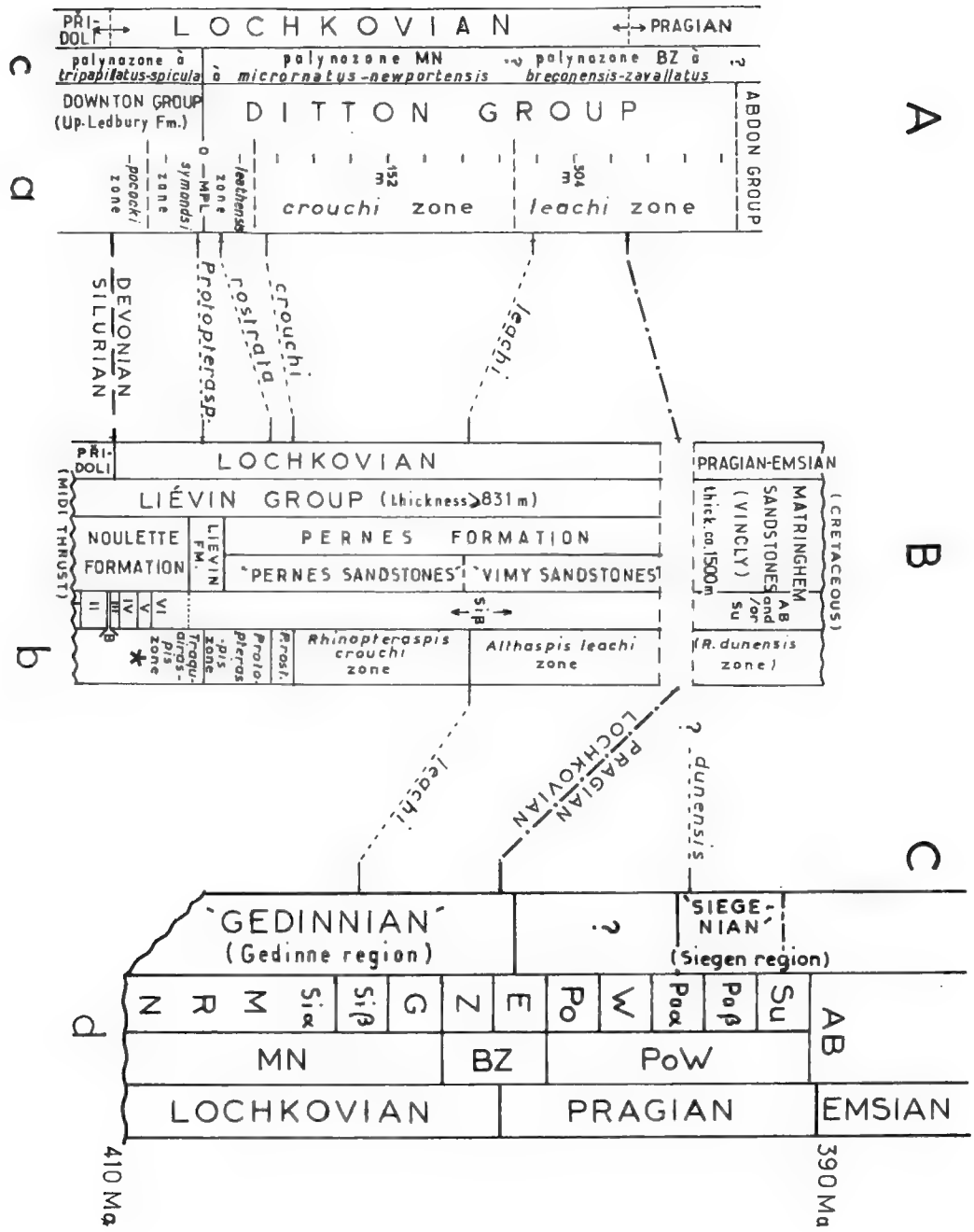
We have indeed six ichthyozones for a time interval of about 18.5 million years (20 Ma after COWIE & BASSETT, 1989, and ODIN & ODIN, 1990; re-evaluated by FORDHAM, 1992: – 408.5 Ma at base Lochkovian, – 390 Ma at base Emsian), so an average duration of ca. 3 Ma per ichthyozone (3.08 "exactly"). This is much less precise than the spore zonation (Fig. 5), but as precise as the conodont succession of the Lower Devonian carbonate sequences which yield seven conodont zones in the Lochkovian-Pragian time interval (HOUSE, 1988; OLIVER & CHLUPAC, 1991; FORDHAM, 1992).

A major problem remains to be solved, viz., to correlate the vertebrate and spore-based succession to the conodont-graptolite-dacryoconarid-based succession. The latter was used to calibrate the sea-level curves of various continental platforms of Euramerica (DENNISON, 1985), Australia and SW Siberia (TALENT & YOLKIN, 1987), and the Canadian Cordillera (MORROW & GELDSETZER, 1988). A high sea-level is in evidence in the mid-Lochkovian uppermost *eurekaensis* conodont zone (Fig. 6). It might be that the acme of the vertebrate fauna at the lower *crouchi* zone of Artois (Fig. 3) is related to that high stand, but it has to be demonstrated. On another hand the impoverishment of the vertebrate fauna of the upper *leachi* and lower *dunensis* zones (Figs. 3, 4) might be related to the low sea-level in the upper Lochkovian-Pragian (Fig. 6) [However this review is mainly based upon agnathan taxic data and should be extended to gnathostomes as well].

FIG. 4 — Synthetic stratigraphy of the Lower Devonian sequence of Ardenne (Belgium) and part of the Rhenish Slate Massif (Germany). a, chronostratigraphy and spore zonation of STEEMANS (1989, and *in* STREEL *et al.*, 1987). b, distribution of the spore-dated vertebrate localities (faunal lists after BLIECK & JAHNKE, 1980; BLIECK, 1982a, b; BLIECK & GOUJET, 1991). c, lithostratigraphy of STREEL *et al.* (1987). d, tentative distribution of other vertebrate localities which are not dated by spores. Note that the Lower Devonian series may be more than 3.500 m thick, particularly in the Arville region.

Synthèse stratigraphique du Dévonien inférieur d'Ardenne (Belgique) et d'une partie du massif schisteux rhénan (Allemagne). a, chronostratigraphie et zones de spores de STEEMANS (1989, et in *STREEL* et al., *1987). b, répartition des localités à Vertébrés datées par spores (listes fauniques d'après BLIECK & JAHNKE, 1980 ; BLIECK, 1982a, b ; BLIECK & GOUJET, 1991). c, lithostratigraphie de STREEL* et al. *(1987). d, essai de répartition des autres localités à Vertébrés qui ne sont pas datées par spores.*

Notez que la série d'âge Dévonien inférieur peut dépasser les 3.500 m en épaisseur, en particulier dans la région d'Arville.



A
B
C
a
b
c
d
PŘI-DOLÍ
LOCHKOVIAN
PRAGIAN
polynozone à tripapillatus-spicula
polynozone MN à micrornatus-newportensis
polynozone BZ à breconensis-zavallatus
DOWNTON GROUP (Up. Ledbury Fm.)
DITTON GROUP
ABDON GROUP
pococki zone
symondsi zone
MPL zone
leathensis
crouchi zone
leachi zone
152 m
304 m
DEVONIAN
SILURIAN
Protopteraspis
rostrata
crouchi
leachi
PŘI-DOLÍ
LOCHKOVIAN
LIÉVIN GROUP (thickness ≥ 831 m)
NOULETTE FORMATION
LIÉVIN FM.
PERNES FORMATION
'PERNES SANDSTONES'
'VIMY SANDSTONES'
(MIDI THRUST)
II
III
IV
V
VI
Siβ
Traquairaspis zone
Protopteraspis zone
Rhinopteraspis crouchi zone
Althaspis leachi zone
PRAGIAN-EMSIAN
MATRINGHEM SANDSTONES (VINCLY)
thick. ca. 1500 m
AB and/or Su
(CRETACEOUS)
(R. dunensis zone)
leachi
PRAGIAN
LOCHKOVIAN
? dunensis
'GEDINNIAN' (Gedinne region)
?
'SIEGENIAN' (Siegen region)
N
R
M
Siα
Siβ
G
Z
E
Po
W
Poα
Poβ
Su
AB
MN
BZ
PoW
LOCHKOVIAN
PRAGIAN
EMSIAN
410 Ma
390 Ma

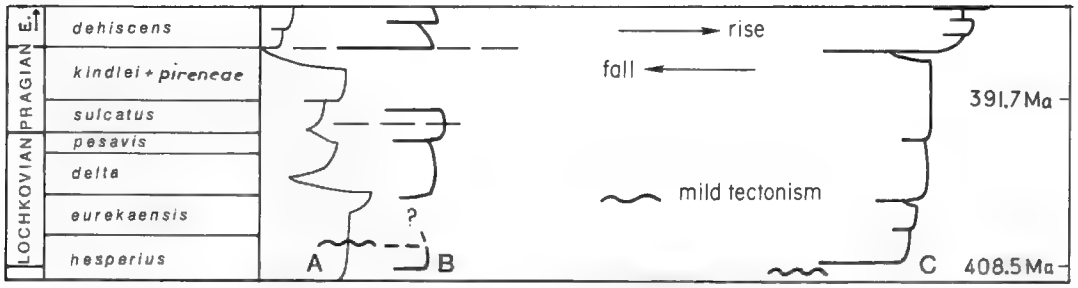


FIG. 6. — Qualitative eustatic curves for (A) Euramerica, (B) Australia, (C) SW Siberia, after DENNISON (1985) and TALENT & YOLKIN (1987, Fig. 5, modified according to OLIVER & CHLUPAC, 1991, for the conodont biozones).
Abbr.: E. = lower Emsian. Radiochronometric data after FORDHAM (1992).

Courbes eustatiques qualitatives pour (A) l'Euramérique, (B) l'Australie, (C) la Sibérie du SW, d'après DENNISON (1985) et TALENT & YOLKIN (1987, Fig. 5, modifiée selon OLIVER & CHLUPAC, 1991, pour les biozones de Conodontes).
Abrév. : E. = Emsien inférieur. Données radiochronologiques d'après FORDHAM (1992).

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FIG. 5. — Biostratigraphical correlation between the Lower Devonian sequences of the Welsh Borderland (A), Artois (B), and the Ardenne-Rhenish Slate Massif (C), after figures 3 and 4, and BLIECK & JANVIER (1989, Fig. 11 corrected), with the fish-zones of (a) BALL & DINELEY (1961) (b) BLIECK & JANVIER (1989), and the spore zones of (c) RICHARDSON & MCGREGOR (1986), (d) STREEL *et al.* (1987). Time calibration after COWIE & BASSETT (1989) and ODIN & ODIN (1990).
* *Traquairaspis* zone: see remark on Fig. 3 and in text.

Corrélations biostratigraphiques entre les séries du Dévonien inférieur de la Bordure Galloise (A), d'Artois (B), et du massif ardenno-rhénan (C), d'après les figures 3 et 4, et BLIECK & JANVIER (1989, Fig. 11 corrigée), avec les zones de Vertébrés de (a) BALL & DINELEY (1961), (b) BLIECK & JANVIER (1989), et les zones de spores de (c) RICHARDSON & MCGREGOR (1986), (d) STREEL et al. (1987). Données radiochronologiques d'après COWIE & BASSETT (1989) et ODIN & ODIN (1990).
* *Zone à* Traquairaspis *: voir la remarque de la figure 3 et le texte.*

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Vertebrate microfauna from the Devonian/Carboniferous boundary stratotype at La Serre, Montagne Noire (Hérault, France)

by Claire DERYCKE, Alain BLIECK and Susan TURNER
(Contribution to IGCP 328 "Palaeozoic Microvertebrates")

Abstract. — Vertebrate microremains have been prepared by acid leaching from oolitic limestone beds at the Devonian/Carboniferous boundary stratotype of La Serre, southeastern Montagne Noire, southern France. They all come from the lowermost Carboniferous beds 89 to 99, *i.e.* the *sulcata* and *kockeli-dentilineatus* conodont zones. Most remains are of elasmobranchs: *Symmorium* sp., *Stethacanthus?* sp., Ctenacanthidae gen. et sp. indet., *Phoebodus* cf. *P. australiensis*, *Thrinacodus ferox*, *Protacrodus* cf. *P. vetustus*, *P.* sp., Elasmobranchii gen. et sp. indet., types A-C; with a few actinopterygian teeth. The assemblage correlates well with other Upper Devonian-Lower Carboniferous localities from the USA, western and eastern Europe, southeast Asia, China, Morocco and Australia.

Keywords. — Ichthyoliths, Devonian/Carboniferous boundary, stratotype, Montagne Noire (France), biostratigraphical correlation, systematics, elasmobranchs, actinopterygians.

La microfaune de Vertébrés du stratotype de la limite Dévonien/Carbonifère à La Serre, Montagne Noire (Hérault, France)

Résumé. — Plusieurs niveaux de calcaire oolitique du stratotype de la limite Dévonien/Carbonifère, à La Serre (Montagne Noire SE, France méridionale), ont livré par attaque acide des microrestes de Vertébrés. Ils proviennent des bancs 89 à 99, datés de la base du Carbonifère, c'est-à-dire des biozones de Conodontes à *sulcata* et à *kockeli-dentilineatus*. La plupart des microrestes sont ceux d'Élasmobranches : *Symmorium* sp., *Stethacanthus?* sp., Ctenacanthidae gen. et sp. indet., *Phoebodus* cf. *P. australiensis*, *Thrinacodus ferox*, *Protacrodus* cf. *P. vetustus*, *P.* sp., Elasmobranchii gen. et sp. indet., types A-C ; mais quelques dents d'Actinoptérygiens ont aussi été extraites. L'assemblage est très proche de ceux qui ont été récoltés dans des localités du Dévonien supérieur-Carbonifère inférieur des États-Unis, d'Europe occidentale et orientale, d'Asie du sud-est, de Chine, du Maroc et d'Australie.

Mots-clés. — Ichthyolithes, limite Dévonien/Carbonifère, stratotype, Montagne Noire (France), corrélation biostratigraphique, systématique, Élasmobranches, Actinoptérygiens.

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INTRODUCTION

Late Palaeozoic vertebrates are rare in the Montagne Noire where three sections in the Mont Peyroux–Pic-de-Bissous and Cabrières areas have yielded few Devonian acanthodians, cochliodonts, and placoderms. Among the latter, *Melanosteus occitanus* LELIÈVRE & GOUJET (*in* LELIÈVRE *et al.*, 1987) from the upper Frasnian Kellwasserkalk facies of La Serre Formation,

at La Serre trench C, is the best preserved species and contributes interesting features to the debate on phylogenetic relationships of selenosteid pachyosteomorph placoderms.

Acid leaching of diverse conodont-bearing carbonate rocks of the Devonian sequence of this region was unsuccessfully carried out by one of us (A. B.) in the search of vertebrate microremains. However, during Dr R. FEIST's (USTL, Montpellier, France) work on the Devonian-Carboniferous (D/C) sequence of Montagne Noire, which bears on defining the D/C boundary stratotype by the Subcommissions on Devonian and Carboniferous Stratigraphy of ICS (IUGS-UNESCO), vertebrate microremains were found with conodonts by Dr G. FLAJS (RWTH, Aachen, Germany) in the basal Carboniferous beds (FLAJS *et al.*, 1988; PAPROTH *et al.*, 1991). At the same time, efforts of one of us (S.T.) to organise Palaeozoic microvertebrate experts' activities led to the IGCP Project 328 (TURNER, 1991-92). One of the topics of this project is the D/C boundary vertebrate stratigraphy, and thus the present study.

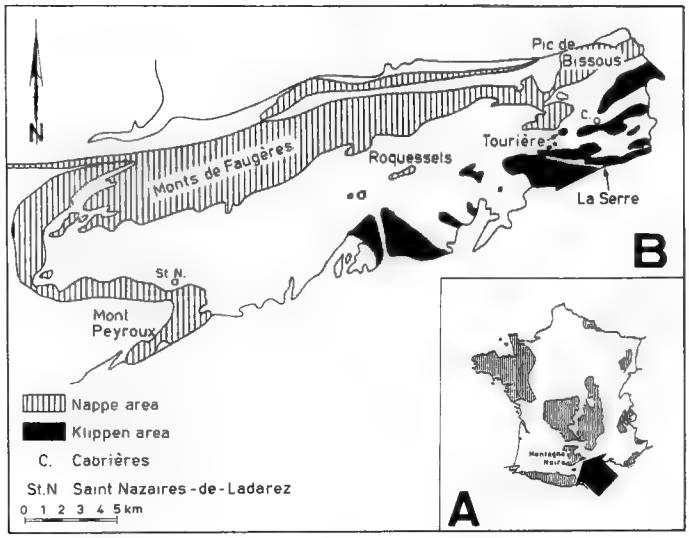
GEOLOGICAL SETTING

The Montagne Noire is located in southern France, at the southern edge of the Central Massif west of the Alps. It is part of the southern Hercynian fold belt of Western Europe (Fig. 1A). There is a very complicated tectonic structure with nappes and klippen on the southeastern flank. La Serre is located within the klippen area ("Écailles de Cabrières"; Fig. 1B). These klippen correspond to olistolites in the syn– and post-tectonic Hercynian (Visean to Namurian) wildflysch of the Mont Peyroux – Pic-de-Bissous nappe area (ENGEL *et al.*, 1978, 1979, 1982). The reconstructed sedimentary sequence of the klippen shows a thick series of Lower Ordovician to Lower Carboniferous rocks more than 1000 m thick and without significant gaps. The Middle to Upper Devonian and Lower Carboniferous beds of this sequence are chiefly limestones, with a dominant uppermost Devonian to lowermost Carboniferous nodular-limestone facies ("Griottes").

In general, the upper Famennian-lower Tournaisian beds are not present in the klippen (e.g. at Tourière, Fig. 1B) where the succession is interrupted by a few decimeters of argillites re-

FIG. 1. — Location of the Devonian/Carboniferous boundary stratotype at La Serre, southeastern Montagne Noire, France. A, location of Montagne Noire among the Hercynian massifs of France (hatched); B, location of La Serre in the klippen area ("Écailles de Cabrières") of southeastern Montagne Noire; C, the reference section La Serre trench E' with distribution of index conodonts and trilobites [species *A. (Phillibole) crispus)* and *Carbonocoryphe (Winterbergia?) funirepa* come from the neighbouring sections La Serre trench G and Col-de-l'Orte, respectively], and environmental interpretation of some depositional and faunal elements (after FLAJS & FEIST, 1988, Figs. 1, 5, 6). White: oolitic limestones, dark grey: various other limestones; light grey: siliciclastics. Vertebrate microremains have been prepared from beds 89 to 99.

Localisation du stratotype de la limite Dévonien/Carbonifère à La Serre, au sud-est de la Montagne Noire, France. A, place de la Montagne Noire parmi les massifs hercyniens de France (hachurés) ; B, place de La Serre dans la région des klippes ("Écailles de Cabrières") du sud-est de la Montagne Noire ; C, coupe de référence de la tranchée E de la Serre, avec distribution des conodontes marqueurs et des Trilobites [les espèces A. (Phillibole) crispus *et* Carbonocoryphe (Winterbergia ?) funirepa *proviennent des coupes voisines de la Serre, tranchée G, et du Col de l'Orte respectivement], avec interprétation environnementale de quelques éléments sédimentaires et fauniques (d'après FLAJS & FEIST, 1988, figs 1, 5, 6). En blanc : calcaires oolithiques ; en gris foncé : autres calcaires ; en gris clair : siliciclastites. Les microrestes de Vertébrés ont été extraits des niveaux 89 à 99.*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Pic de Bissous
C.
Tourière
Roquessels
Monts de Faugères
La Serre
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C. Cabrières
St.N Saint Nazaires-de-Ladarez
0 1 2 3 4 5 km
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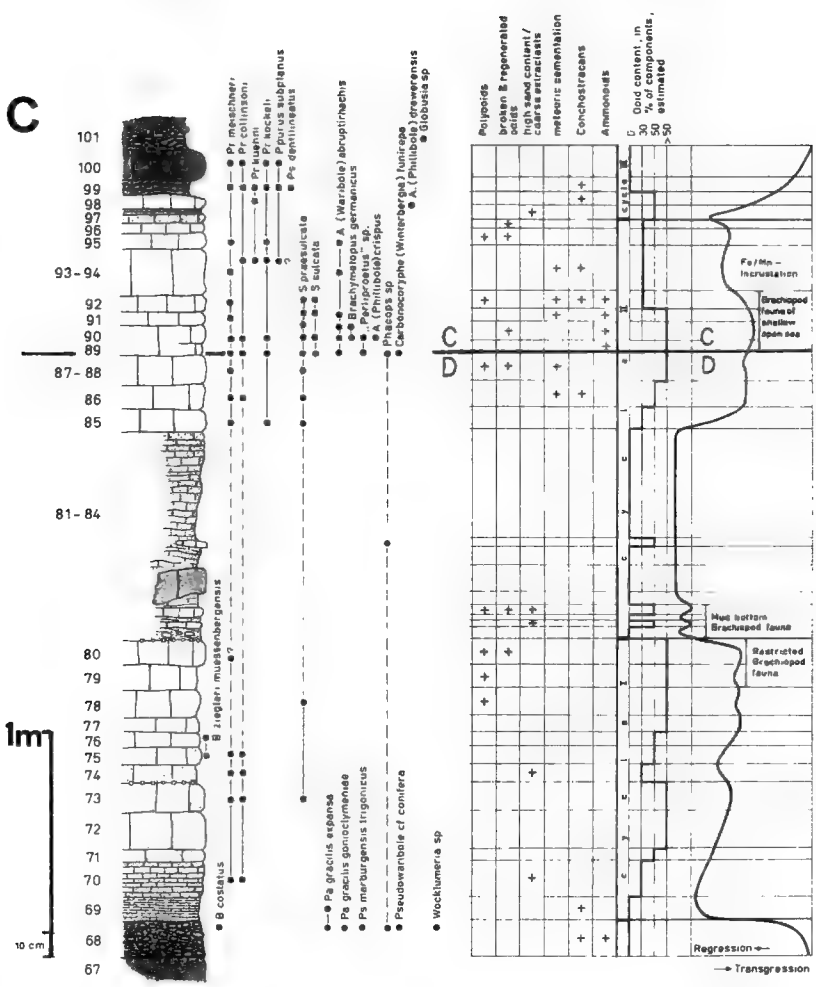
C
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1m
10 cm
Pr meischneri
Pr collinsoni
Pr kuehni
Pr kockeli
P purus subplanus
Ps dentilineatus
S praesulcata
S sulcata
A (Waribole) abruptirhachis
Brachymatopus germanicus
"Periproetus" sp.
A (Phillibole) crispus
Phacops sp
Carbonocoryphe (Winterbergia) funiceps
A. (Phillibole) drewerensis
Globusia sp
B ziegleri muessenbergensis
B costatus
Pa gracilis expansa
Pa gracilis gonioclymeniae
Ps marburgensis trigonicus
Pseudowaribole cf conifera
Wocklumeria sp
Polypoids
broken & regenerated ooids
high sand content / coarse extraclasts
meteoric cementation
Conchostracans
Ammonoids
Ooid content, in % of components, estimated
0
30
50
>50
Fe/Mn - Incrustation
Brachiopod fauna of shallow open sea
Mud bottom Brachiopod fauna
Restricted Brachiopod fauna
Regression
Transgression

presenting, at least in part, the equivalent of the Hangenberg Shale of the Rhenish Slate Massif (Germany). This shale constitutes a widespread facies type at the D/C boundary and may correspond to a worldwide regressive eustatic event (references *in* FEIST, 1983, 1990; FEIST & FLAJS, 1987; FLAJS & FEIST, 1988). The only exception to this gap in the klippen area of Cabrières is at La Serre Hill where uppermost Devonian clymeniid-bearing rocks are overlain by D/C transitional biodetrital calcoolites yielding protognathodid conodonts and trilobites, followed by lower Tournaisian marly nodular limestones. The La Serre trench E' (dug on the southern slope of the hill) shows an uninterrupted carbonate sequence across the D/C boundary in the upper part of the middle member of the Griottes Limestone; the section is not overturned here, and schistosity and tectonic complications are absent. It has yielded a fauna of conodonts and trilobites (Fig. 1C; FLAJS & FEIST, 1988), but also cephalopods, brachiopods, corals, foraminifers, algae, conchostracans, bryozoans, gastropods, bivalves, ostracodes, and microproblematica (LEGRAND-BLAIN & MARTINEZ-CHACON, 1988; SEMENOFF-TIAN-CHANSKY, 1988; VACHARD, 1988; see a complete faunal list *in* FEIST, 1990, Fig. 35; PAPROTH *et al.*, 1991, Fig. 6).

The D/C boundary transitional beds correspond to "a typical near-shore environment under normal marine conditions" as indicated by the "abundant ooids, cortoids and benthic organisms occurring throughout the section" (FLAJS & FEIST, 1988: 65). They correspond to an oolitic limestone interval within the "basinal", pelagic limestone facies of the sequence. This oolitic interval contains "very rich, reworked conodont associations which are representative of the entire Upper Devonian" (*ibid.*, p. 54-55), but the authors concluded that the youngest elements in the associations allow "unequivocal stratigraphical dating". In contrast, "macrofossils, such as trilobites or brachiopods, have not been reworked" (*ibid.*: see also LEGRAND-BLAIN & MARTINEZ-CHACON, 1988: 119-120). However, many of the calcareous microfossils are indicative of the upper Famennian ("Strunian" of authors: VACHARD, 1988: 140-141), so the possibility of their transportation cannot be excluded; however, "as they occur, at La Serre, within the *sulcata* Zone, they extend into the lowermost Carboniferous" (*ibid.*, p. 141).

Vertebrate microremains have been extracted from beds 89 to 99, *i.e.* from the lowermost Carboniferous *sulcata* (beds 89 to 98) and *kockeli-dentilineatus* (bed 99) conodont zones (Fig. 1C). No vertebrate has been obtained from below the D/C boundary. It should be noted that at La Serre the vertebrates seem to be restricted to the oolitic facies. As part of the fauna is reworked, it may be that the vertebrates are reworked as well. This could explain their restricted stratigraphical range and it would be in accord with their poor preservation.

SYSTEMATICS

Only a few scales and teeth of gnathostome fishes have been obtained. They are not well preserved. However, they extend to southern France and its D/C boundary stratotype a vertebrate assemblage already known worldwide. As these remains are scarce, no thin section has been made; all determinations are based on external morphology. The scanning electron micrographs were made on a Cambridge Stereoscan 240. The specimens are deposited in the vertebrate collection of the University of Lille, Villeneuve d'Ascq, France (CVUL).

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838

PRELIMINARY SYSTEMATIC REMARKS

In most recent papers on isolated Palaeozoic elasmobranch microremains authors use ZANGERL's (1981) classification (see also CARROLL, 1988). However, instances of non-compliance with the rules of the International Code of Zoological Nomenclature (ICZN: RIDE *et al.*, 1985) are present in that classification.

The superfamilies Ctenacanthoidea, Hybodontoidea and Edestoidea are incorrectly attributed. Because of the coordinate status of family-group names (ICZN art. 36), the following corrections have to be made: Ctenacanthoidea Zangerl, 1981, should be Ctenacanthoidea Dean, 1909, based on the family Ctenacanthidae Dean, 1909; Hybodontoidea Zangerl, 1981, should be Hybodontoidea Owen, 1846, based on the family Hybodontidae Owen, 1846 (*in* CAPPETTA, 1987); and Edestoidea Hay, 1930 (*in* ZANGERL, 1981) should be Edestoidea Jaekel, 1899, based on the family Edestidae Jaekel, 1899.

The family name Phoebodontidae is attributed to WILLIAMS (1979) by ZANGERL (1981: 54). However, "WILLIAMS, 1979" is a Ph. D. dissertation (ref. *in* ZANGERL, 1981: 109) which does not constitute a publication [ICZN art. 9 (11)]. The authorship of this family thus should be given as Phoebodontidae Williams *in* ZANGERL, 1981, or strictly as Phoebodontidae Zangerl, 1981, although it was formally established by WILLIAMS (1985: 124).

The family name Diplodoselachidae is attributed to DICK (MS) by ZANGERL (1981: 64), but DICK's paper was published the same year (DICK, 1981); the correct authorship citation thus is Diplodoselachidae Dick, 1981.

What also seems strange when looking at the proposed phylogenetic relationships of the Eugeneodontida ZANGERL (1981, Fig. 102; Eugeneodontiformes Zangerl, 1981, *in* CAPPETTA, 1987), is to have the ordinal name Eugeneodontida created after the family Eugeneodontidae which is included in the superfamily Caseodontoidea. It would have been preferable to name the order after one of its constituent superfamilies, the Caseodontoidea or Edestoidea. Or why not Edestida, which existed prior to ZANGERL's work (1981: 74)?

Another point to be made is that some of ZANGERL's superfamilies or orders are not based on families; e.g. Hybodontoidea (ZANGERL, 1981: 56; but family Hybodontidae Owen, 1846 exists: CAPPETTA, 1987), Protacrodontoidea (regarded by ZANGERL, 1981: 61, as equivalent to family Tamiobatidae [Tamiobatidae Hay, 1902 after GLIKMAN *in* OBRUCHEV, 1964; but not Tamiobatidae Glikman, 1964 after ZANGERL]; but *Tamiobatis* is considered "not presently identifiable as to order" by ZANGERL, 1981: 102), Desmiodontida (*ibid.*, p. 62), Coronodontida (*ibid.*, p. 68; but family Coronodontidae Harris, 1950 exists: WILLIAMS, 1985: 132), Petalodontida (ZANGERL, 1981: 94, without family name for the non-pristodontid petalodonts, although family Petalodontidae Newberry & Worthen, 1866 does exist), Squatinactida (*ibid.*, p. 101; but family Squatinactidae is used by LUND, 1990: 4). It is, of course, always easier to criticize than to create a coherent systematics (mainly when isolated, fragmentary microremains are concerned), but users of ZANGERL's system should be aware of these discrepancies. However, the lack of families in ZANGERL's systematics is not simply a matter of omissions. The discrepancies are due to legi-

timate differences of opinion which stem primarily from the inadequate record of the groups concerned. The Petalodontidae is a good example, the name indeed exists but nobody knows which genera it should include (J. ZIDEK, written comm., 1992). We follow ZANGERL's classification, slightly modified.

Order SYMMORIIDA Zangerl, 1981
Family SYMMORIIDAE Dean, 1909
Genus **SYMMORIUM** Cope, 1893

Symmorium sp.
(Fig. 2; Pls III, D; IV, B-C)

REFERRED MATERIAL. —Three isolated teeth from beds 95 (CVUL 13) and 99 (CVUL 15-16).

DESCRIPTION AND DISCUSSION

These three teeth are typically cladodont, *i.e.* multicuspidate with a tall central and shorter lateral cusps. The kidney-shaped base with the labial side strongly concave just below the main cusp (labial sinus) is the main character of *Symmorium* (see the amended generic diagnosis of WILLIAMS, 1985: 103). The central cusp is tall, lingually curved, and labially bears sharp and narrow longitudinal cristae which converge in CVUL 16 (Pl. IV, C). A cutting edge (carina) is noticeable on the main cusp which is labially flattened and lingually strongly convex. Shorter lateral cusps number one to three pairs, the second one being slightly taller. Their cross sections are circular.

All cusps are arranged along the labial margin of the base. The characters noted above are those of *S. reniforme* (see WILLIAMS, 1985). However, as we have not seen the original material of *S. reniforme*, and because our specimens are microscopic (max. 1.5mm long) and poorly preserved, we prefer staying in open nomenclature. According to WILLIAMS (1985: 107), *Symmorium* teeth possess an additional feature, "The inner of the lateral pairs [of denticles of the crown]... is produced outward so that a line drawn connecting the centers of the cusps would describe a broad, low, "W" (Pl. 7, Fig. 2)" as one of our specimens (Pl. III, D). One tooth (Fig. 2a) shows two noticeable basolabial facets underneath the two lateral cusps, which is characteristic of the genus *Symmorium* (ZIDEK, 1992: 152). On the two other teeth, it is not so evident because one (Fig. 2b) is worn and the other (Fig. 2c) is recovered by recrystallisations.

Two teeth (Pl. IV, B-C) possess an inclined main cusp; this asymmetry should be an indication of the position in the mouth. The base of CVUL 15 (Pl. IV, B) is pierced by two large foraminae on the lingual and aboral faces, connected by a canal which is exposed due to wear. It looks like an hemiaulacorhize base *sensu* CASIER (1947). *Symmorium* sp. described by LONG (1990) from the late Famennian of northern Thailand differs from our sample mainly by the shape of the base, which in the Thailand form is dumbbell-shaped. The specimens illustrated by WANG (1989, Pl. 28, 3; Pl. 30, 5) from the Dapoushang section of south China also belong to *Symmorium*.

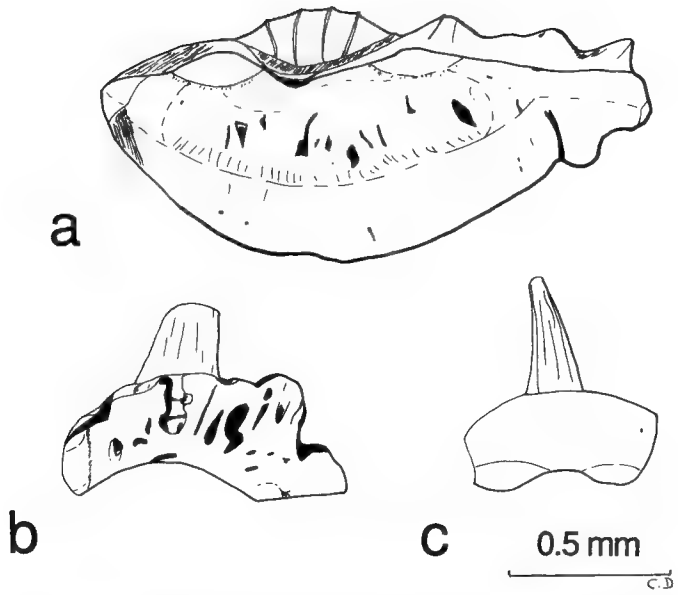

FIG. 2. — *Symmorium* sp., isolated teeth, aboral views. a, CVUL 13 from bed 95, same as Pl. III, D, labial margin faces up. b, CVUL 15 from bed 99, same as Pl. IV, B, labial margin faces down. c, CVUL 16 from bed 99, same as Pl. IV, C, labial margin faces down.

Symmorium *sp., dents isolées, vues aborales ou basales. a, CVUL 13 du banc 95, même spécimen que pl. III, D, le bord labial est tourné vers le haut. b, CVUL 15 du banc 99, même spécimen que pl. IV, B, le bord labial est orienté vers le bas. c, CVUL 16 du banc 99, même spécimen que pl. IV, C, le bord labial est tourné vers le bas.*

Family STETHACANTHIDAE Lund, 1974
Genus **STETHACANTHUS** Newberry, 1889

Stethacanthus? sp.
(Fig. 3; Pls I, C; II, A-B; IV, D-F)

REFERRED MATERIAL. — Isolated teeth from beds 89 (CVUL 3), 92-93 (CVUL 6-7), 99 (CVUL 17-19).

DESCRIPTION AND DISCUSSION

CVUL 3 (Pl. I, C) is a cladodont tooth with a main central cusp and three pairs of lateral cusps, all arched lingually. The first and the third pairs of lateral cusps are shorter than the second pair. The vertical cristae do not bifurcate near the base and are not accompanied by intercalated cristae as is often the case in *Symmorium*. The two surfaces are separated by a cutting edge (carina). The base is well drawn, triangular and punctuated by some foramina. On the labial margin, it is produced into a rectangular basolabial articulating boss below the main

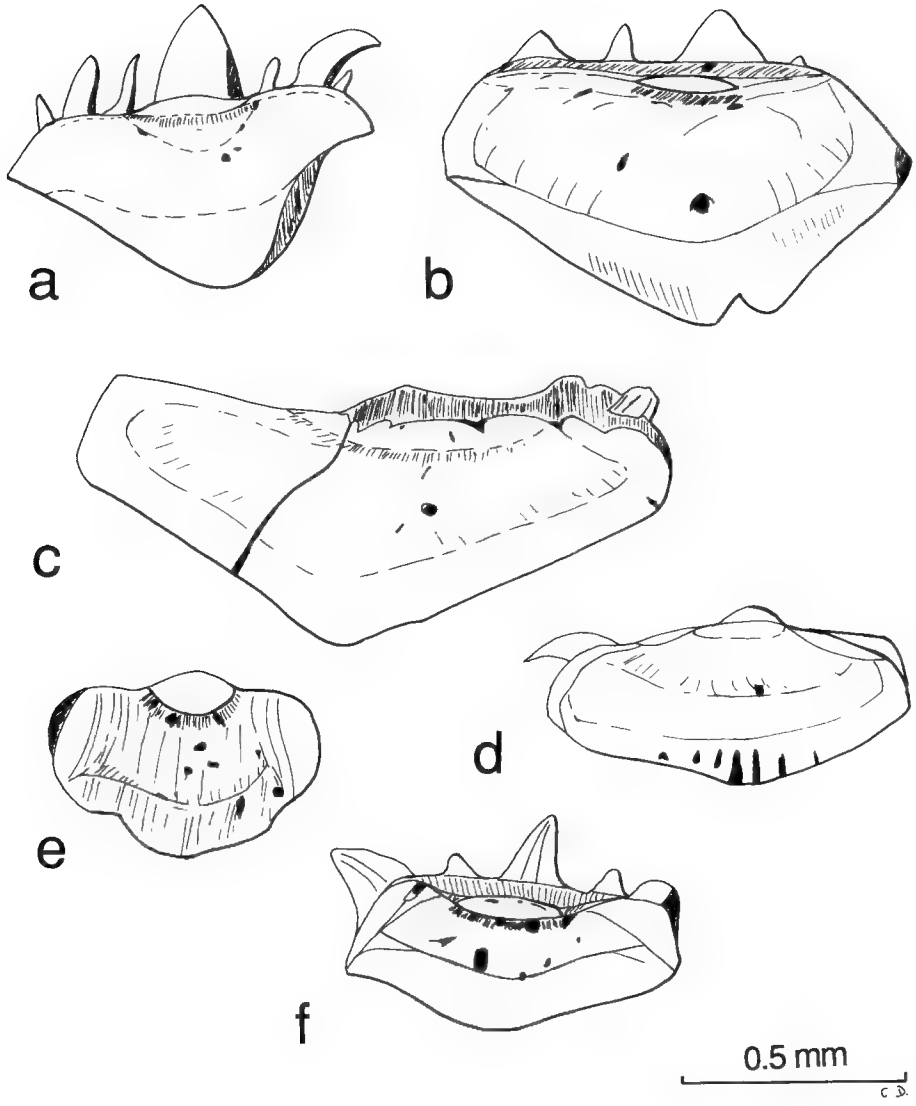

FIG. 3. — *Stethacanthus?* sp., isolated teeth, aboral views, labial margins face up. a, CVUL 3 from bed 89, same as Pl. I, C. b, CVUL 7 from bed 92-93, same as Pl. II, B. c, CVUL 6 from bed 92-93, same as Pl. II, A. d, CVUL 17 from bed 99, same as Pl. IV, D. e, CVUL 18 from bed 99, same as Pl. IV, E. f, CVUL 19 from bed 99, same as Pl. IV, F.

Stethacanthus? *sp., dents isolées, vues aborales ou basales, les bords labiaux sont tous orientés vers le haut. a, CVUL 3 du banc 89, même spécimen que pl. I, C. b, CVUL 7 du banc 92-93, même spécimen que pl. II, B. c, CVUL 6 du banc 92-93, même spécimen que pl. II, A. d, CVUL 17 du banc 99, même spécimen que pl. IV, D. e, CVUL 18 du banc 99, même spécimen que pl. IV, E. f, CVUL 19 du banc 99, même spécimen que pl. IV, F.*

cusp and towards the inner margins of the first lateral cusps (Fig. 3). This is a distinctive character of *Stethacanthus* according to WILLIAMS (1985). Above the lateral cusps is a distinct crest. However, a coronal view shows lingually on the base a button (lingual articulating boss) and a boundary delineating the crown.

As is often the case in *Stethacanthus*, the two teeth from bed 92-93 (Pl. II, A-B) have five cusps, all of them broken. The central cusp is the tallest, and the lateral pair is taller than the intermediate pair, as is apparent from the diameters of the cross sections. The cristae are the most evident on the lingual surface. The carina is not well defined, especially in CVUL 7 (Pl. II, B). The rectangular basolabial boss is visible just below the central cusp of CVUL 7 (Pl. II, B). This tooth has a strongly concave aboral surface, which bears a central big foramen. Another foramen is located just below the central cusp, and a third one is in the middle of the lingual face of the base, in effect dividing the lingual articulating boss (Fig. 3b). The base appears to be hemiaulacorhize *sensu* CASIER (1947).

Three other teeth, from bed 99 (Pl. IV, D-F), have less broken but more worn cusps. The longitudinal cristae are still visible on the central cusp of CVUL 17 (Pl. IV, D), but not on the others. The bases are subtriangular or five-sided, with a prominent lingual boss and numerous small foramina (Fig. 3d-f). A similar tooth with a sharply triangular base was illustrated by WANG (1989, Pl. 30, 5-6, "*Cladodus*" sp.) and thought to be a new genus by TURNER & WANG (1992).

Superorder EUSELACHII Hay, 1902
Order CTENACANTHIFORMES Nelson, 1976
Superfamily CTENACANTHOIDEA Dean, 1909
Family CTENACANTHIDAE Dean, 1909

CTENACANTHIDAE gen. et sp. indet.
(Fig. 4b-c; Pls II, C; III, A)

REFERRED MATERIAL. — Two isolated scales from beds 92-93 (CVUL 8), 95 (CVUL 10).

DESCRIPTION AND DISCUSSION

These are scarce, isolated, partially broken ctenacanthid scales (*sensu* REIF, 1978). The first one, from bed 92-93 (Pl. II, C), bears longitudinal ridges that anteriorly split into two or three branches. The posterior concave surface which forms the neck is punctuated by a line of well developed foramina (Fig. 4b). The scale is wider than high and the base is concave.

The second scale, from bed 95 (Pl. III, A), is attributed to Ctenacanthidae with some doubt because it has a very convex bony base (Fig. 4c). Its crown bears bifurcating ridges and its anterior edge is located on the diagonal axis of the square base. The ridges radiate from the anterior edge to the posterolateral corners of the crown.

We compare our scales with the ctenacanthid scale type of REIF (1978) which occurs in *Ctenacanthus costellatus* and *Goodrichthys eskdalensis*. As very few publications deal with isolated scales, our taxonomic assignment must be considered tentative.

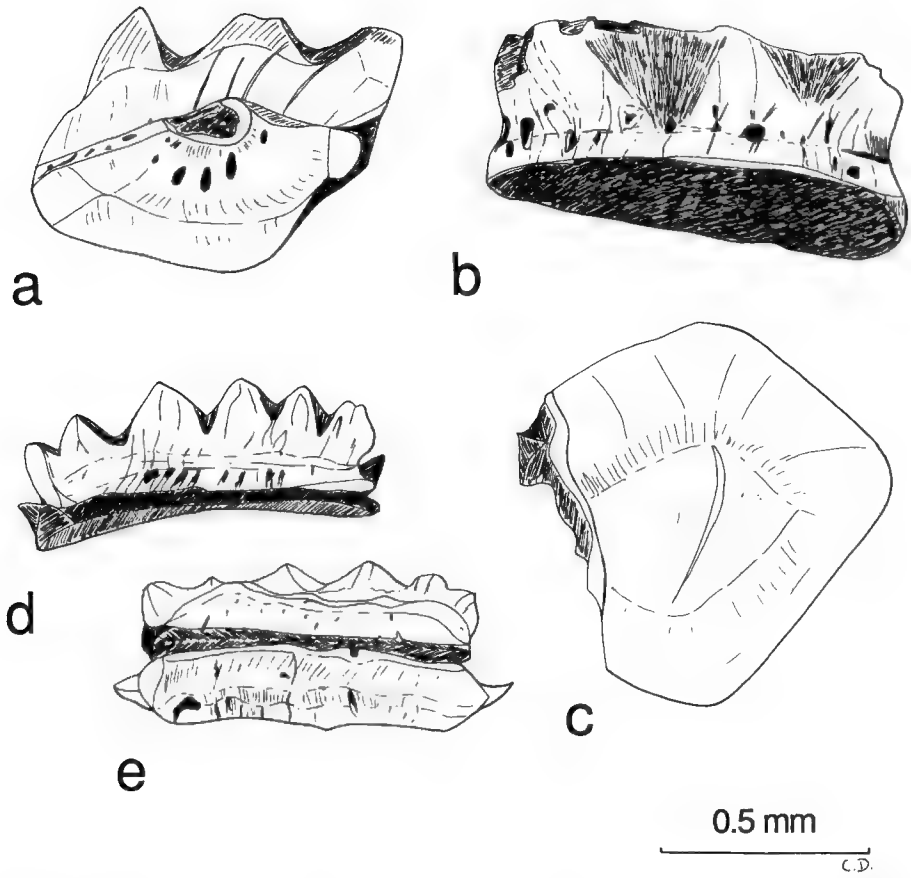

FIG. 4. — a, *Protacrodus* sp., tooth CVUL 12 from bed 95, same as Pl. III, C, basolabial view. b-c, Ctenacanthidae gen. et sp. indet., scales (b) CVUL 8 from bed 92-93, same as Pl. II, C, linguobasal view, and (c) CVUL 10 from bed 95, same as Pl. III, A, aboral view. d-e, *Protacrodus* cf. *P. vetustus*, associated teeth CVUL 22 from bed 99, same as Pl. IV, I, labial or lingual (d) and aboral (e) views.

a, Protacrodus *sp., dent CVUL 12 du banc 95, même spécimen que pl. III, C, vue basolabiale. b-c, Ctenacanthidae gen. et sp. indet., écailles (b) CVUL 8 du banc 92-93, même spécimen que pl. II, C, vue linguobasale, et (c) CVUL 10 du banc 95, même spécimen que pl. III, A vue aborale ou basale. d-e,* Protacrodus *cf.* P. vetustus, *dents imbriquées CVUL 22 du banc 99, même spécimen que pl. IV, I, vues labiale ou linguale (d) et aborale ou basale (e).*

Family PHOEBODONTIDAE Williams *in* Zangerl, 1981
Genus **PHOEBODUS** St. John & Worthen, 1875

Phoebodus cf. **P. australiensis** Long, 1990
(Fig. 5; Pl. IV, G-H)

REFERRED MATERIAL. — Two fragmentary teeth from bed 99 (CVUL 20-21).

DESCRIPTION AND DISCUSSION

These teeth lack small intermediate cusps. The lingual surfaces of the three cusps are ornamented by five coarse cristae. The central cusp leans slightly towards one of the lateral cusps. The base resembles a half-ellipse (Fig. 5b). Under the main cusp is a prominent basolabial boss. A longitudinal groove (Fig. 5b) with some foramina is also apparent. These teeth are very similar to *P. australiensis* Long (1990, Figs. 2-4; see also GINTER, 1990, Pl. I, 3-11) but the cusps are more densely cristated on the tooth sides and their tips are not as pointed. On our material the lingual torus shows more foramina (Fig. 5a) than on *P. australiensis* Long (1990). *P. australiensis* is based on material from Thailand. LONG (1990) named this species *australiensis* because of its resemblance to other teeth from Australia (*Phoebodus* cf. *P. politus in* TURNER, 1982, Fig. 6 A-B; but also from China: *Phoebodus politus in* WANG & TURNER, 1985, Pls II, 1; III, 2). However, it appears that the teeth from Australia and some from China differ from *P. australiensis* in having more massive and erect cusps (see comments by GINTER, 1990: 73-74; GINTER & IVANOV, 1992; TURNER & WANG, 1992). So *P. australiensis* is known from Thailand, China, Poland, France, and probably also Germany (after GINTER, 1990: 73; see GROSS, 1973, Pl. 34, 3), whereas the Australian and some of the Chinese *Phoebodus* are not *australiensis* ! Nevertheless, few teeth from Guizhou, China, which WANG (1989, Pls 28, 2, 5; 29, 3-4; 30, 1; Pl. 31, 4) called "*Cladodus* spp.", correspond to *P. australiensis* teeth (see also TURNER & WANG, 1992), and are most like those from La Serre. This species appears to be typical of the latest Famennian to early Tournaisian interval.

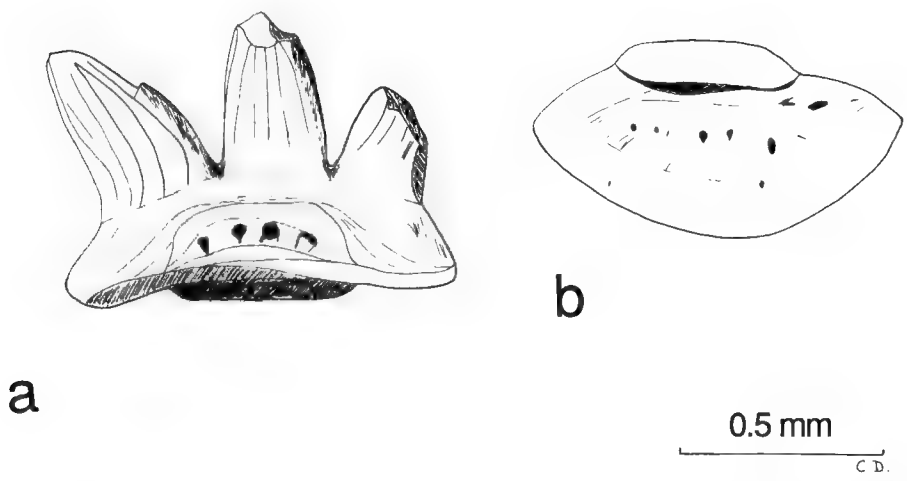

FIG. 5. — *Phoebodus* cf. *P. australiensis*, isolated tooth CVUL 20 from bed 99, same as Pl. IV, G. a, lingual view. b, aboral view, labial margin faces up.

Phoebodus *cf.* P. australiensis, *dent isolée CVUL 20 du banc 99, même spécimen que pl. IV, G. a, vue linguale. b, vue aborale ou basale, le côté labial est orienté vers le haut.*

Genus **THRINACODUS** St. John & Worthen, 1875

Thrinacodus ferox (Turner, 1982)
(Pls III, B; IV, A)

1982 *Harpago ferox* Turner, p. 118-123, Figs. 2-5.
1983 *Harpagodens* Turner, p. 38.
1990 *Thrinacodus (Harpagodens) ferox* Turner, 1982 [sic]: Long, 1990: 61-62, Fig. 5 H, J-M.

Referred material. — Two isolated teeth from beds 95 (CVUL 11) and 99 (CVUL 14).

Description and discussion

These microscopic grappling-hook-like teeth have three fang-shaped cusps whose lingual surface is gently cristated. The base is elongate, twice as long as wide. It is punctuated by a single foramen at the tip. This species appears to be ubiquitous from mid-Famennian to late Tournaisian.

Superfamily Protacrodontoidea Zangerl, 1981
Family Protacrodontidae Zangerl, 1981
Genus **PROTACRODUS** Jaekel, 1921

Protacrodus cf. **P. vetustus** Jaekel, 1921
(Fig. 4d-e; Pl. IV, I)

Preliminary remarks. — The name Protacrodontoidea was created by Zangerl (1981: 61). According to ICZN article 36a (Ride *et al.*, 1985: 76), this name is also established with the same author and date for any other taxon based upon the name-bearing type at other ranks in the family group with appropriate change of suffix. So Protacrodontidae Wang & Turner, 1985 is a junior synonym of Protacrodontidae Zangerl, 1981.

Referred material. — Two associated teeth from bed 99 (CVUL 22).

Description and discussion

These united teeth, as *P. vetustus*, have labio-lingually compressed crowns and a crest joining all the cusps (see, e.g. *in* Zangerl, 1981). The main, more-or-less central, conical cusp is flanked by two or three smaller cusps on both sides. All cusps are strongly ridged. The tooth base bears numerous large foramina essentially on its lateral faces (Fig. 4d).

Protacrodus sp.
(Fig. 4a; Pl. III, C)

Referred material. — One isolated tooth from bed 95 (CVUL 12).

Description and discussion

The crown shows wide cusps slightly cristated and linked by a sharp crest. It is rather high and labio-lingually compressed. The labial side of the base is not offset against the crown,

whereas lingually the base is extended. A broken boss is present underneath the central cusp around which large foramina are organised in a depression. The labial and lingual sides of the base show small foramina (Fig. 4a).

ELASMOBRANCHII gen. et sp. indet.

Type A
(Fig. 6c; Pls I, D; IV, J)

REFERRED MATERIAL. — Two isolated denticles from beds 89 (CVUL 4) and 99 (CVUL 23).

DESCRIPTION

These composite denticles are ovoid in coronal view and bear five or six cusps, arranged in two rows, with the smallest cusp at the end of each row. Each cusp is triangular, smooth, with a rounded tip, but the cusps of CVUL 23 (Pl. IV, J) are more compressed. Both denticles have a concave base. These denticles are probably branchial or pharyngeal.

Type B
(Pl. IV, K)

REFERRED MATERIAL. — One isolated scale from bed 99 (destroyed during preparation).

DESCRIPTION

This scale bears three pointed cusps. Each cusp has a central, triangular portion which may be either convex or concave, and thin lateral extensions.

Type C
(Fig. 6a-b; Pl. I, A-B)

REFERRED MATERIAL. — Two broken teeth from bed 89 (CVUL 1 and 2).

DESCRIPTION AND DISCUSSION

The base is approximately kidney-shaped, with a concave labial side and a convex lingual side. Some foramina are visible on the aboral surface. The lingual surface of the cusps bears widely spaced, converging cristae of varying length, whereas the labial face is nearly smooth. The two faces are separated by a cutting edge (carina). The base bears three massive cusps. At first glance, they appear to be asymmetrical with a lateral, pathological projection. However, the projection seems to correspond to a broken cusp. Even though these teeth are reminiscent of *Symmorium* (e.g. WILLIAMS, 1985), the more widely spaced longitudinal cristae on the cusps and their asymmetry differ from that genus. The bases are subtriangular and one shows some foramina at its lingual margin (Fig. 6a).

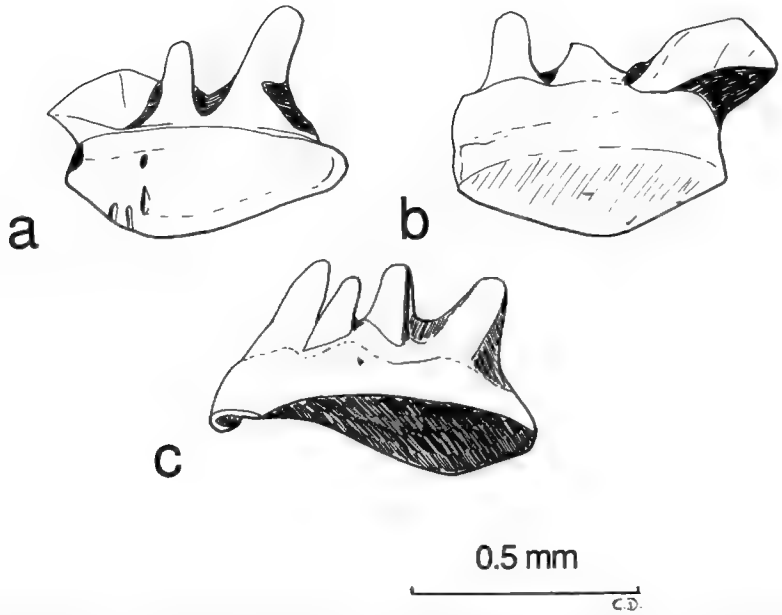

FIG. 6. — Elasmobranchii gen. et sp. indet. from bed 89. a, Type C, tooth CVUL 1, same as Pl. I, A, basolabial view. b, Type C, tooth CVUL 2, same as Pl. I, B, basolabial view. c, Type A, branchial denticle CVUL 4, same as Pl. I, D, lateral view.

Elasmobranchii gen. et sp. indet. du banc 89. a, Type C, dent CVUL 1, même spécimen que pl. I, A, vue basolabiale. b, Type C, dent CVUL 2, même spécimen que pl. I, B, vue basolabiale. c, Type A, denticule branchial CVUL 4, même spécimen que pl. I, D, vue latérale.

Class OSTEICHTHYES Huxley, 1880
Subclass ACTINOPTERYGII Klein, 1885
ACTINOPTERYGII gen. et sp. indet.

Type A
(Pl. I, E)

REFERRED MATERIAL. — A fragmentary tooth from bed 89 (CVUL 5).

DESCRIPTION

This fragment of curved, conical tooth is densely covered by thin, dashed lines of cristae converging toward the tip. These lines obliquely approach the convex side which is broken but clearly curved.

Type B
(Pl. II, D)

REFERRED MATERIAL. — A fragment of tooth from bed 92-93 (CVUL 9).

DESCRIPTION

This tooth is, as the latter, densely covered by dashed alignments of small cristae. It still has its smooth cap of acrodin (Pl. II, D1). An SEM enlargement shows the short, fusiform longi-

tudinal cristae of each line to alternate with those of the adjacent lines (Pl. II, D2). This is characteristic of the texture of ganoin (SCHULTZE, 1977).

BIOSTRATIGRAPHY AND CORRELATION

Despite the paucity and restricted range of microvertebrates at the La Serre D/C section, some biostratigraphical value can be discerned. The assemblage consists almost entirely of chondrichthyans, which is typical of Late Devonian and Early Carboniferous microvertebrate assemblages. Equivalent macrofaunas are generally poor in shark remains. The La Serre assemblage comprises teeth of phoebodont, symmoriid, stethacanthid and protacrodontid sharks, and scales of probable ctenacanthid sharks. Associated are a few unusual actinopterygian teeth, which might represent a new palaeoniscoid genus. This assemblage compares well with Late Devonian and Early Carboniferous assemblages known from Europe [northern France and southern Belgium (CRASQUIN, 1984), Germany (GROSS, 1973; MADER & SCHULTZE, 1987), Russia and Poland (GINTER, 1990; GINTER & IVANOV, 1992)], and has elements in common with roughly contemporaneous sites in Morocco (DERYCKE, 1992), southeast Asia (LONG, 1990; WANG & TURNER, 1985), and the USA (KIETZKE & LUCAS, 1992).

Symmorium reniforme Cope has long been known from the Lower to Upper Carboniferous of the USA (WILLIAMS, 1985; ZANGERL, 1981). More recently, the genus has been recorded from the Late Devonian to Early Carboniferous of Thailand and south China, the Lower Carboniferous of Germany, the Late Devonian of Poland and Russia (refs. above) and the late Pennsylvanian of New Mexico (ZIDEK, 1992). Stethacanthids appear by the mid-Famennian in Poland, and are found in the Carboniferous of the USA, Europe, Thailand, China and Australia (WILLIAMS, 1985). Phoebodont teeth are proving to be a useful biostratigraphical tool for this time interval (GINTER, 1992; GINTER & IVANOV, 1992). They first appear in the Givetian of the USA and possibly of Australia, and continue across the D/C boundary. *Phoebodus australiensis*, *P. limpidus* and *P.* sp. cf. *P. australiensis* seem to be typical of the latest Famennian to Early Carboniferous in Thailand, south China, Poland and the Urals (*op. cit.*) as well as at La Serre. *Thrinacodus ferox*, probably a close relative of the phoebodonts, is often found in association with the above species in the Late Devonian (appearing with the *marginifera* conodont zone) to late Tournaisian deposits. It has been reported from the latest Devonian of the USA (KIETZKE & LUCAS, 1992) and the Lower Carboniferous of Australia, China, Turkey, parts of western Europe, Poland and Russia, and is an easily recognizable fossil for this interval. Protacrodont teeth occur frequently with phoebodont teeth and *Thrinacodus ferox* and generally have the same Famennian to Early Carboniferous range, although in Australia they have only been found in Devonian rocks. The assemblage described by KIETZKE & LUCAS (1992) from the D/C boundary in the Sacramento Mountains, New Mexico, also contain *Phoebodus* ("*P. politus*"), *Protacrodus* sp. cf. *P. vetustus*, protacrodonts similar to the ones from Australia and China, and *Thrinacodus*. The authors assigned a Late Devonian age to the fauna, although the presence of orodonts and *Helodus* may indicate a younger age. Possibly this is another case of an assemblage right on the boundary, with incoming Carboniferous forms.

The La Serre assemblage lacks acanthodian scales of the *Acanthodes* type commonly found at most other sites of this time interval, and bony-fish remains are exceedingly sparse. This may

of course be due to the small amount of material available for study.

Of interest is the possible facies correlation which this assemblage suggests with a platformal oolitic limestone containing *Siphonodella* conodonts, trilobites, ammonoids, numerous brachiopods, corals, foraminifers, algae and so on (PAPROTH *et al.*, 1991). A microassemblage of the same age from the Nanbiancun D/C boundary section contained a very different fauna (WANG Cheng-yuan *in* YU, 1988, Pl. 87). At La Serre, the palaeoecological-geochemical analysis of brachiopods suggests "slightly dysaerobic conditions coupled with slightly lower salinities than during deposition of the preceding [latest Devonian] units. [Productivity increased dramatically to new levels accompanied by warmer temperatures and shallowing of the sea"] (BRAND & LEGRAND-BLAIN, 1993)

Overall, the La Serre fauna correlates well with other latest Devonian or earliest Carboniferous faunas, with a slight tip in favour of the Lower Carboniferous sites in Europe and the USA which include forms such as *Symmorium* sp. cf. *S. reniforme*, *Protacrodus* sp. cf. *P. vetustus* and orodontids. This is not surprising as the La Serre ichthyoliths come from the lowermost Carboniferous beds only. *Phoebodus australiensis* is typical of the latest Devonian to earliest Carboniferous interval in Thailand, south China and the Russian platform, and this is the first western European locality for this species.

CONCLUSION

The assemblage from the La Serre D/C boundary section provides a supplementary record of several important sharks which dominated the Late Devonian to Early Carboniferous marginal-marine platforms and pelagic environments of the world. *Thrinacodus* is not known for certain from the Devonian of Europe but in France it is present in the earliest Carboniferous. It is known from the Late Devonian in Morocco, the marginal seas of the presumed north Gondwana shoreline. *Phoebodus australiensis* appears in the mid-Famennian *trachytera* zone and extends into the *expansa-sulcata* zones in southeast Asia and the East European Russian platform [including the Holy Cross Mountains (Poland), Moravia (Czech Republic), Timan, south Urals and Kuznetsk (Russia); HLADIL *et al.*, 1991; GINTER & IVANOV, 1992]. Similarly, the protacrodonts, phoebodonts and stethacanthids, and possibly the other shark groups as well seem to appear during the latest Devonian in the eastern or north Gondwana region, before appearing in Europe and the USA in earliest Carboniferous times. Of course, more research into the Late Devonian microvertebrate faunas of the USA might clarify or nullify this hypothesis.

The elements of the new assemblage constitute a group of rapidly dispersing species. Closer study of their taxonomy and occurrences now being carried out by participants in IGCP 328 is refining their geographic and stratigraphical ranges.

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PLATE I. — Vertebrate microremains from bed 89 at La Serre, trench E' (Montagne Noire, Hérault, France), basal Carboniferous bed, *Siphonodella sulcata* conodont zone, upper part of middle member of Griottes Formation. A-B, Elasmobranchii gen. et sp. indet. Type C, broken teeth CVUL 1 and 2, lingual views. C, *Stethacanthus?* sp., isolated tooth CVUL 3, coronal view. Labial margin faces down. D, Elasmobranchii gen. et sp. indet. Type A, branchial denticle CVUL 4, coronal view. E, Actinopterygii gen. et sp. indet. Type A, broken tooth CVUL 5 in lateral view. All scale bars equal 100 µm ("UM").

Microrestes de Vertébrés du banc 89 de La Serre, tranchée E' (Montagne Noire, Hérault, France), niveau basal du Carbonifère, zone de conodontes à Siphonodella sulcata, *partie supérieure du membre moyen de la Formation des Griottes. A-B, Elasmobranchii gen. et sp. indet. Type C, dents cassées CVUL 1 et 2, vues linguales. C,* Stethacanthus *? sp., dent isolée CVUL 3, vue coronale. Le bord labial est orienté vers le bas. D, Elasmobranchii gen. et sp. indet. Type A, denticule branchial CVUL 4, vue coronale. E, Actinopterygii gen. et sp. indet. Type A, dent cassée CVUL 5, vue latérale. Toutes les échelles métriques correspondent à 100 µm ("UM").*

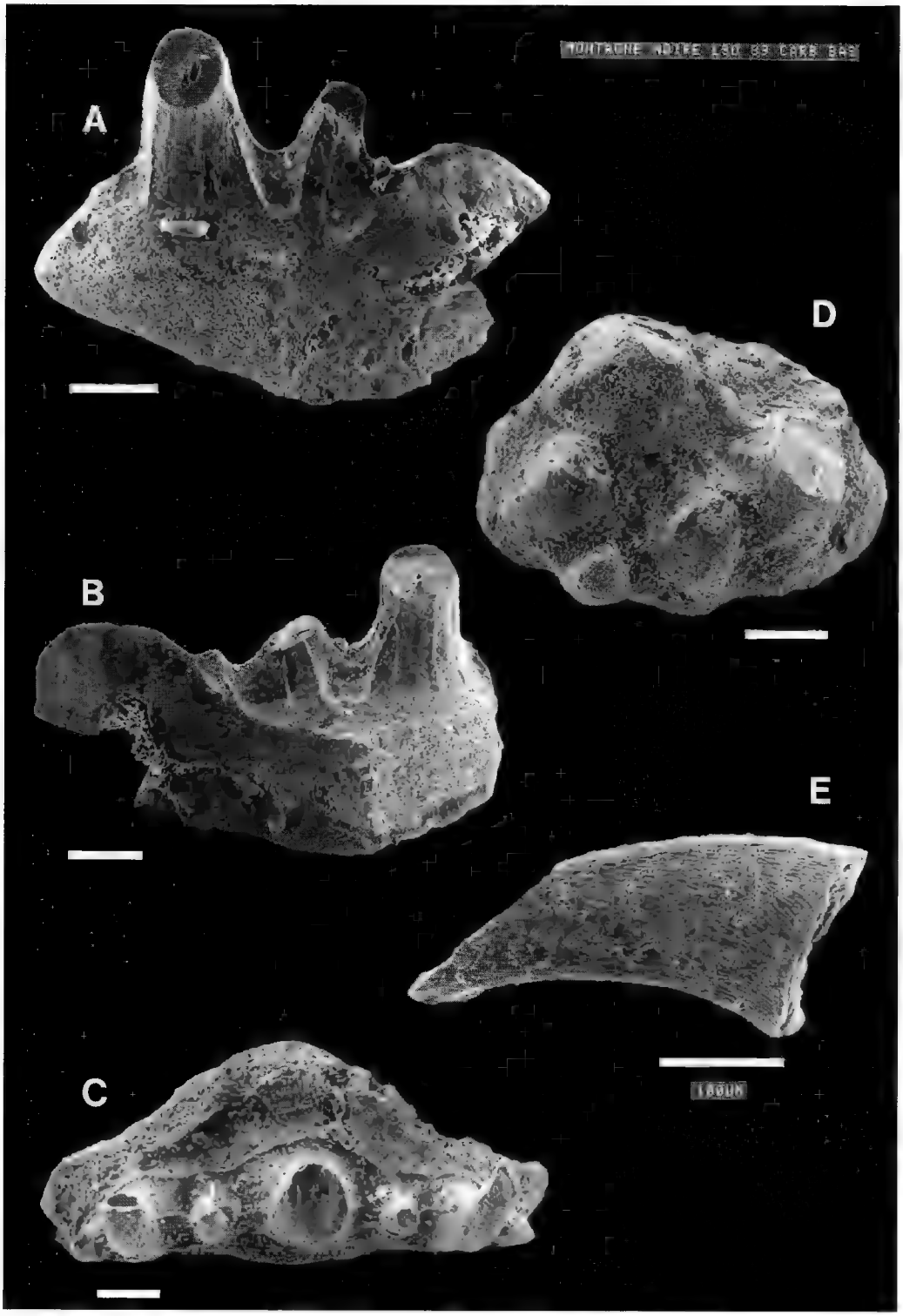

A
B
C
D
E
180UM

PLATE II. — Vertebrate microremains from bed 92-93 at La Serre, trench E' (Montagne Noire, Hérault, France), lowermost Carboniferous, *Siphonodella sulcata* conodont zone, upper part of middle member of Griottes Formation. A-B, *Stethacanthus?* sp., broken teeth CVUL 6 and 7, coronal views. Labial margins face up. C, Ctenacanthidae gen. et sp. indet., scale CVUL 8, coronal view. Anterior margin faces up. D, Actinopterygii gen. et sp. indet. Type B, isolated tooth CVUL 9, coronal view with the acrodin tip (D1) and detail of the ganoin surface (D2). All scale bars are in µm ("UM").

Microrestes de Vertébrés du banc 92-93 de La Serre, tranchée E' (Montagne Noire, Hérault, France), niveau le plus bas du Carbonifère, zone de conodontes à Siphonodella sulcata, *partie supérieure du membre moyen de la Formation des Griottes. A-B,* Stethacanthus? *sp., dents cassées CVUL 6 and 7, vues coronales. Les bords labiaux sont tournés vers le haut. C, Ctenacanthidae gen. et sp. indet., écaille CVUL 8, vue coronale. Le bord antérieur est tourné vers le haut. D, Actinopterygii gen. et sp. indet. Type B, dent isolée CVUL 9, vue coronale avec le capuchon d'acrodine (D1) et un détail de la surface de ganoïne (D2). Toutes les échelles métriques sont en µm ("UM").*

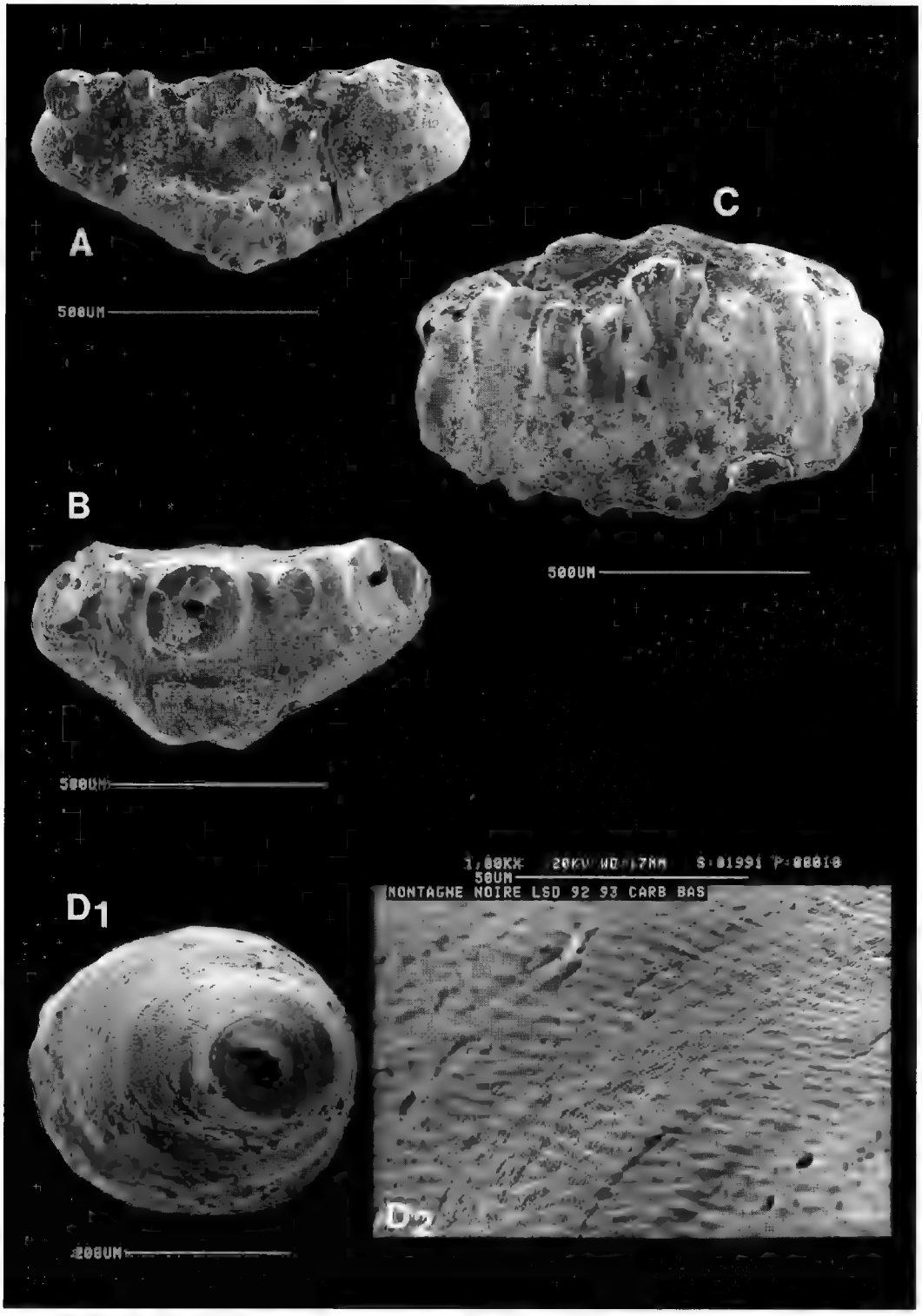

A
500UM
C
500UM
B
500UM
D1
200UM
50UM
MONTAGNE NOIRE LSD 92 93 CARB BAS
D2

PLATE III. — Vertebrate microremains from bed 95 at La Serre, trench E' (Montagne Noire, Hérault, France), lowermost Carboniferous, *Siphonodella sulcata* conodont zone, upper part of middle member of Griottes Formation. A, Ctenacanthidae gen. et sp. indet., scale CVUL 10, coronal view. Anterior margin faces up. B, *Thrinacodus ferox*, isolated tooth CVUL 11, lateral view. C, *Protacrodus* sp., tooth CVUL 12, coronal view. Labial margin faces up. D, *Symmorium* sp., broken tooth CVUL 13, coronal view. Labial margin faces up. All scale bars are in µm ("UM").

Microrestes de Vertébrés du banc 95 de La Serre, tranchée E' (Montagne Noire, Hérault, France), niveau le plus bas du Carbonifère, zone de conodontes à Siphonodella sulcata, *partie supérieure du membre moyen de la Formation des Griottes. A, Ctenacanthidae gen. et sp. indet., écaille CVUL 10, vue coronale. Le bord antérieur est tourné vers le haut. B,* Thrinacodus ferox, *dent isolée CVUL 11, vue latérale. C,* Protacrodus *sp., dent CVUL 12, vue coronale. Le bord labial est orienté vers le haut. D,* Symmorium *sp., dent cassée CVUL 13, vue coronale. Le bord labial est orienté vers le haut. Toutes les échelles métriques sont en* µm *("UM").*

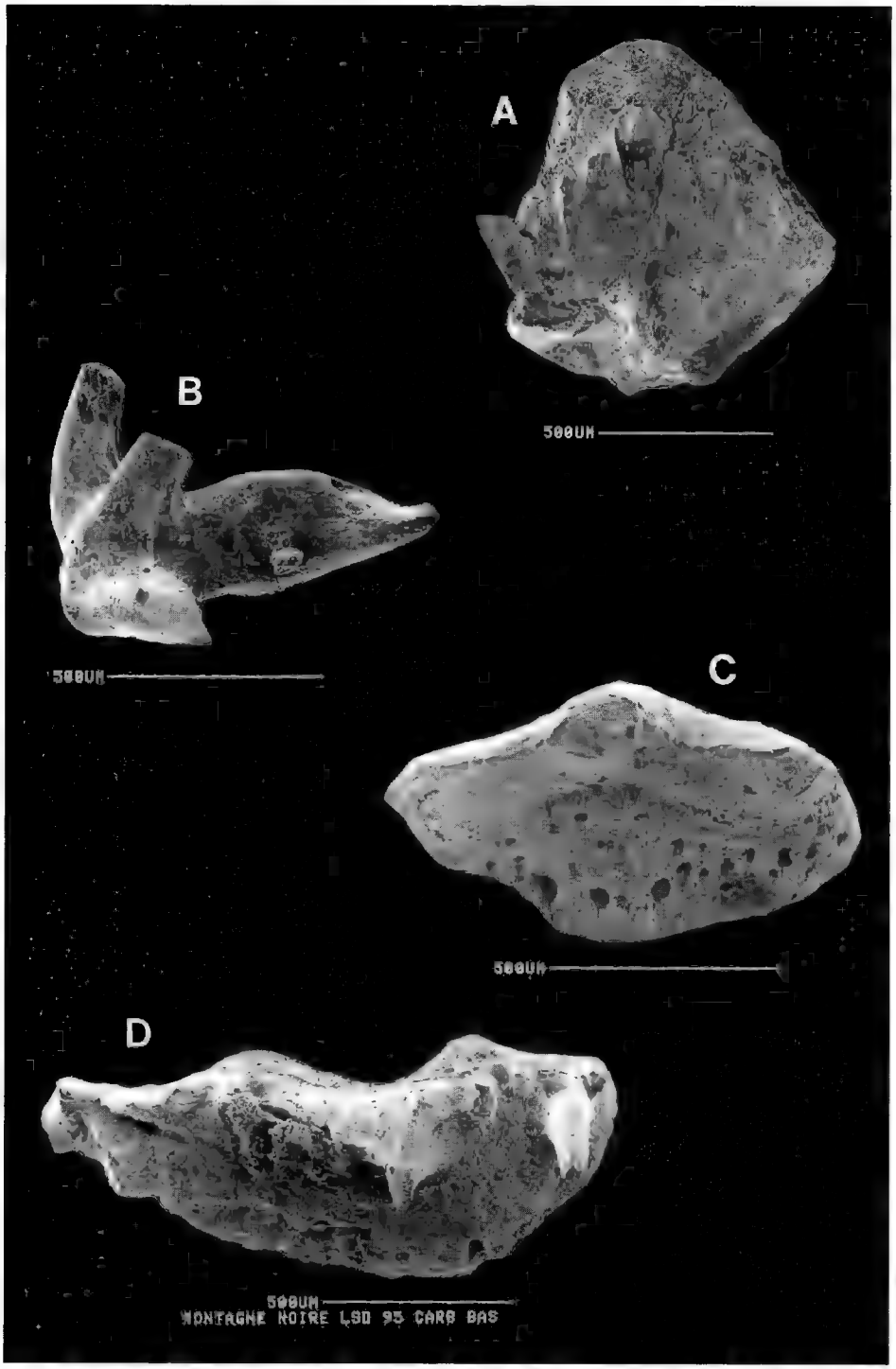
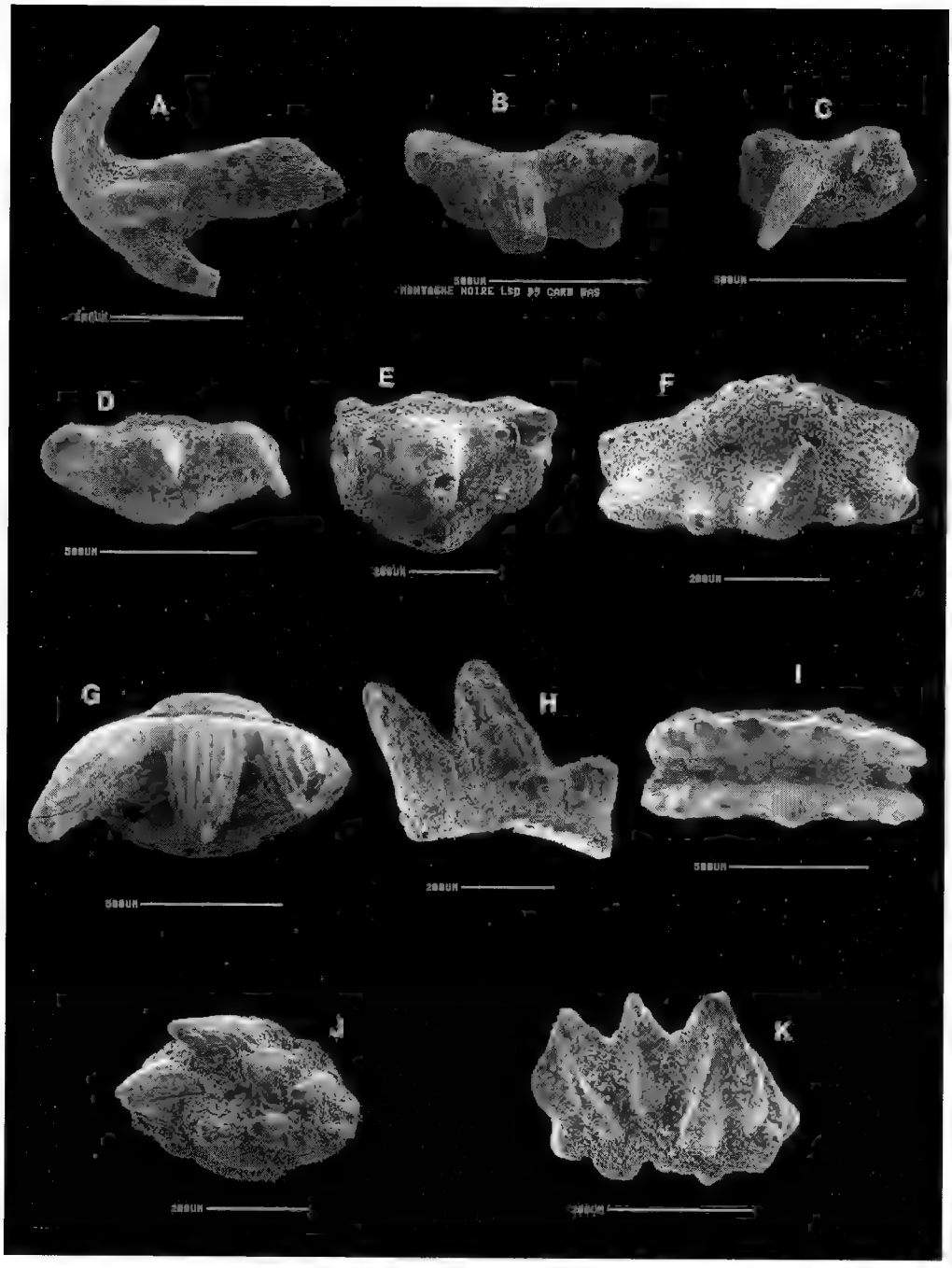

A
500UM
B
500UM
C
500UM
D
500UM
MONTAGNE NOIRE LSD 95 CARB BAS

PLATE IV. — Vertebrate microremains from bed 99 at La Serre, trench E' (Montagne Noire, Hérault, France), lower Carboniferous, *kockeli-dentilineatus* conodont zone, upper part of middle member of Griottes Formation. A, *Thrinacodus ferox*, isolated tooth CVUL 14, nearly coronal view. B-C, *Symmorium* sp., isolated teeth CVUL 15 and 16, coronal views. Labial margins face up. D-F, *Stethacanthus?* sp., isolated teeth CVUL 17, 18, 19, coronal views. Labial margins face up in D-E and down in F. Note the worn surfaces of most cusps. Central cusp in E was broken after preparation. G-H, *Phoebodus* cf. *P. australiensis*, isolated teeth CVUL 20 and 21, coronal (G) and labial (H) views. I, *Protacrodus* cf. *P. vetustus*, two associated teeth CVUL 22, coronal view. J, Elasmobranchii gen. et sp. indet. Type A, isolated branchial denticle CVUL 23, coronal view. K, Elasmobranchii gen. et sp. indet. Type B, isolated scale destroyed during preparation, coronal view. All scale bars are in µm ("UM").

Microrestes de Vertébrés du banc 99 de La Serre, tranchée E' (Montagne Noire, Hérault, France), Carbonifère inférieur, zone de conodontes à kockeli-dentilineatus, *partie supérieure du membre moyen de la Formation des Griottes. A,* Thrinacodus ferox, *dent isolée CVUL 14, vue presque coronale. B-C,* Symmorium *sp., dents isolées CVUL 15 et 16, vues coronales. Les bords labiaux sont tournés vers le haut. D-F,* Stethacanthus? *sp., dents isolées CVUL 17, 18, 19, vues coronales. Les bords labiaux sont orientés vers le haut en D-E et vers le bas en F. Les surfaces de la plupart des cuspides sont usées. La cuspide centrale en E a été cassée en cours de préparation. G-H,* Phoebodus *cf.* P. australiensis, *dents isolées CVUL 20 et 21, vues coronale (G) et labiale (H). I,* Protacrodus *cf.* P. vetustus, *deux dents imbriquées CVUL 22, vue coronale. J, Elasmobranchii gen. et sp. indet. Type A, denticule branchial isolé CVUL 23, vue coronale. K, Elasmobranchii gen. et sp. indet. Type B, écaille isolée détruite pendant la préparation, vue coronale. Toutes les échelles métriques sont en µm ("UM").*


A
B
C
D
E
F
G
H
I
J
K

Bull. Mus. natl. Hist. nat., Paris, 4e sér., **17**, 1995
Section C, n° 1-4 : 487-511.

Upper Givetian and Frasnian ichthyoliths from Bas-Boulonnais (Pas-de-Calais, France): preliminary records

by Claire DERYCKE, Denise BRICE, Alain BLIECK and Nicolas MOURAVIEFF
(Contribution to IGCP 328 "Palaeozoic Microvertebrates")

Abstract. — New finds of Upper Givetian and Frasnian fishes from Boulonnais contribute to project IGCP 328 which aims to create a data base of microremains for biostratigraphical, palaeoecological and palaeobiogeographical correlations. Morphological and histological data are presented to integrate the ichthyoliths in a systematic frame. The composition of the fauna is typical of Upper Devonian times comprising *Symmorium?* sp., *Ctenacanthus* sp. and other chondrichthyan elements; acanthodians are present with *Ptomacanthus?* sp. and *Acanthodes* sp. An inferognathal of *Rhynchodus?* sp. is identified. Actinopterygians are represented by *Moythomasia* sp., and sarcopterygian remains include an undetermined Onychodontida, undet. Porolepiformes and *Spodichthys?* sp. All the previously published and the newly described taxa are situated in the Givetian to Famennian stratigraphical scale of the Ferques inlier. The richest assemblages come from 1) the middle Givetian, lower Blacourt Formation, 2) the uppermost Givetian-lowermost Frasnian (lowermost and lower *Polygnathus asymmetricus* conodont zones), lower Beaulieu Formation, and 3) the upper Frasnian (upper *P. asymmetricus* and *Ancyrognathus triangularis* zones), Ferques Formation. The Blacourt Formation assemblage is dominated by placoderms. The newly described lower Beaulieu Formation assemblage is much poorer in placoderms but richer in chondrichthyans, acanthodians, actinopterygians and sarcopterygians. The Ferques Formation assemblage on the contrary seems to be devoid of sarcopterygians, but placoderms, chondrichthyans, actinopterygians and acanthodians do occur.

Keywords. — Ichthyoliths, Upper Devonian, Boulonnais (France), biostratigraphy, palaeogeography, histology, systematics, placoderms, chondrichthyans, acanthodians, actinopterygians, sarcopterygians.

Ichthyolithes du Givétien supérieur et du Frasnien du Bas-Boulonnais (Pas-de-Calais, France) : données préliminaires

Résumé. — Une nouvelle microfaune de poissons en provenance du Givétien supérieur et du Frasnien du Boulonnais est présentée dans le cadre du projet PICG 328 qui vise à mettre en place une banque de données à usages biostratigraphique, paléoécologique et paléobiogéographique. Les informations morphologiques et histologiques sont utilisées conjointement afin d'intégrer les ichthyolithes dans un cadre systématique. La composition de la faune est typique du Dévonien supérieur puisqu'elle comprend *Symmorium*? sp., *Ctenacanthus* sp. et d'autres éléments de Chondrichthyens, les Acanthodiens *Ptomacanthus*? sp. et *Acanthodes* sp. Un inférognathal de *Rhynchodus*? sp. est identifié. Les Actinoptérygiens sont représentés par *Moythomasia* sp. Finalement, quelques restes de Sarcoptérygiens sont figurés : un Onychodontida et des Porolépiformes indéterminés ainsi que *Spodichthys*? sp. L'ensemble des taxons déjà publiés et de nouvelles découvertes sont situés dans l'échelle stratigraphique du Givétien au Famennien du massif de Ferques. Les niveaux les plus riches proviennent 1) de la partie inférieure de la Formation de Blacourt d'âge givétien moyen ; 2) de la partie inférieure de la Formation de Beaulieu d'âge givétien terminal-frasnien basal (zones de conodontes basale et inférieure à *Polygnathus asymmetricus*) ; 3) de la Formation de Ferques d'âge frasnien supérieur (zones à *P. asymmetricus* supérieure et à *Ancyrognathus triangularis*). La faune des niveaux 1 est dominée par les Placodermes. Celle des niveaux 2 est beaucoup plus pauvre en Placodermes mais plus riche en Chondrichthyens, Acanthodiens, Actinoptérygiens et Sarcoptérygiens. Enfin la faune des niveaux 3, apparemment dépourvue de Sarcoptérygiens, renferme des Placodermes, des Chondrichthyens, des Actinoptérygiens et des Acanthodiens.

Mots-clés. — Ichthyolithes, Dévonien supérieur, Boulonnais (France), biostratigraphie, paléogéographie, histologie, systématique, Placodermes, Chondrichthyens, Acanthodiens, Actinoptérygiens, Sarcoptérygiens.

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INTRODUCTION

In northern France, a zone of Palaeozoic outcrops is found in Boulonnais-Artois-Ardenne along Hercynian lineaments. The Midi Fault, the most important overthrust of the region, divides it in two. The Boulonnais inlier is part of the northern parautochthonous unit (including the Brabant Massif and the Namur Synclinorium) whereas the southern Artois inliers and the Ardenne Massif are parts of the allochthonous unit (including the Dinant Synclinorium). In the Parautochthon, the Middle Devonian to Westphalian D layers, which are without schistosity, are conformable on the schistous Cambro-Silurian substratum of Brabant (RAOULT *et al.*, 1984, 1985; RAOULT & MEILLIEZ, 1986, 1987; RAOULT, 1986; KHATIR *et al.*, 1989). Jurassic and Cretaceous levels overlay the Palaeozoic. By means of erosion and tectonic movements, Devonian and Carboniferous rocks outcrop in the Ferques Inlier (Fig. 1).

Six lithological units are defined in the Devonian of Ferques (BRICE *et al.*, 1979). The fauna comes from four of them: Blacourt, Beaulieu, Ferques and Hydrequent Formations, dated uppermost Givetian to Frasnian and corresponding to the *Polygnathus ensensis* to *Ancyrognathus triangularis* conodont zones (BRICE, 1988a; we have not compared this zonation with ZIEGLER & SANDBERG's (1990) one). These formations are famous for their abundant invertebrate fauna composed of brachiopods, rugose and tabulate corals, conodonts, bryozoans, bivalves, trilobites, crinoids, stromatoporoids, as well as vertebrates and plant remains (BRICE, 1988b).

The Blacourt Formation is interpreted as a platform deposit. The fauna from the Beaulieu Formation indicates an open marine, shallow littoral, perirefal environment in its middle part (Noces Member). The Ferques Formation corresponds to a shallow marine environment and was deposited under variable and sometimes strong energy conditions (tempestites), essentially in a brachiopod-rich level of the Bois Member. The upper part of the Hydrequent Formation presents a concentrate sedimentation (BRICE, 1986, 1988a-b).

Few ichthyofaunal remains have been recorded so far in the Boulonnais, since MURCHISON's (1840) attribution of Devonian levels on the basis of a fish scale and an "ichthyodorulite". They correspond to placoderms, acanthodians, actinopterygians and sarcopterygians. For the first time, chondrichthyans are described from the Devonian of Boulonnais. The biostratigraphical distribution of some species is uncertain. Biostratigraphical and biogeographical comparisons were made with Scotland and the Baltic States (LELIÈVRE *et al.*, 1988).

MATERIALS

The material was collected during a Palaeontological Association field meeting in November 1976 by one of us (N. M.) studying conodonts. They come mainly from shaly carbonate rock samples. They are registered in the collection of vertebrates of the University of Lille (CVUL). Below is the list of samples with their geographical and stratigraphical origins (Fig. 2).

BLACOURT FORMATION

Couderousse Member, nodules in a grey marl, Caffiers-Ferques railway cut, sample BLN19 (Upper Givetian, upper-middle *varcus* zone).

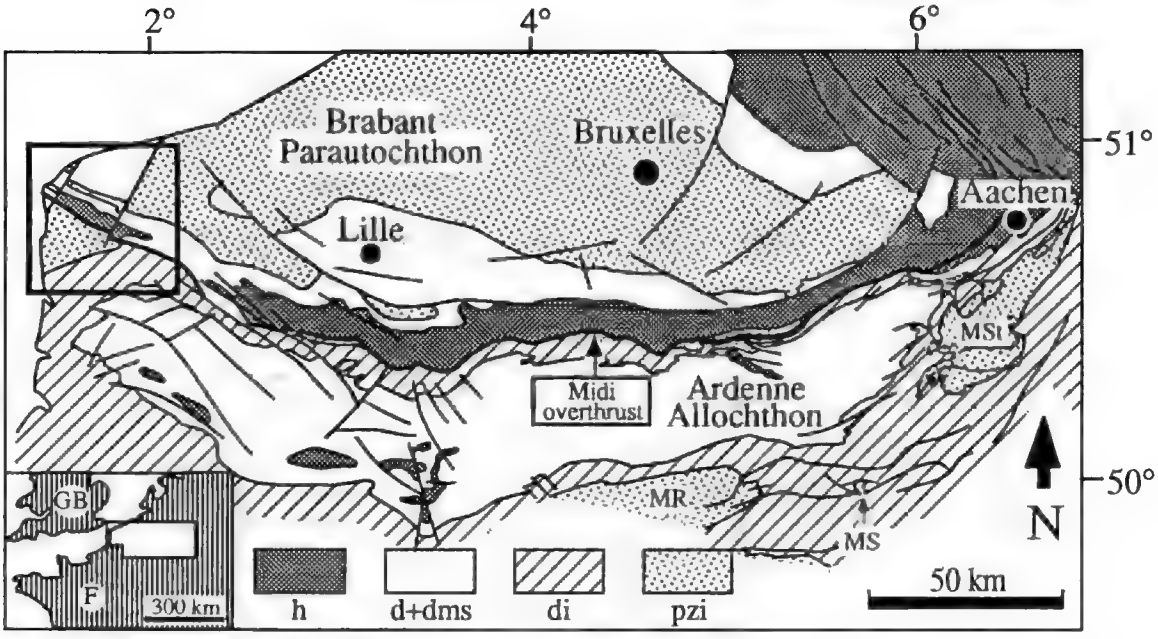

FIG. 1. — Geological setting of the Boulonnais (squared) at the western end of the northern French Hercynian belt (sub-Mesozoic geology after KHATIR, 1990).
Abbr.: h, Carboniferous; d+dms, Dinantian and Middle + Upper Devonian; di, Lower Devonian; pzi, Lower Palaeozoic.
Cadre géologique du Boulonnais (encadré) à l'extrémité ouest de la structure hercynienne du nord de la France (écorché inframésozoïque d'après KHATIR, 1990).
Abrév. : h, Carbonifère ; d + dms, Dinantien et Dévonien moyen et supérieur ; di, Dévonien inférieur ; pzi, Paléozoïque inférieur.

BEAULIEU FORMATION

Cambresèque Member, "La Cédule limestone", upper part of the SW way of the Banc Noir quarry (BLN1, 1II, 1B; uppermost Givetian, lowermost *asymmetricus* zone).

Cambresèque Member, SW entry of the Griset quarry (BLN3) and SW way at entry of the Banc Noir quarry (BLN4 and 5) (lower Frasnian, lower *asymmetricus* zone).

Upper Noces Member, unit "p", Caffiers-Ferques railway cut (BLN20; lower Frasnian, middle *asymmetricus* zone).

FERQUES FORMATION

Bois Member, Bois quarry, thick brachiopod-bearing bed (BLN16) and La Parisienne quarry (BLN7-17) (Frasnian, upper *asymmetricus* zone).

La Parisienne Member, upper *Hexagonaria* level, La Parisienne quarry (BLN9; Frasnian, upper *asymmetricus* zone).

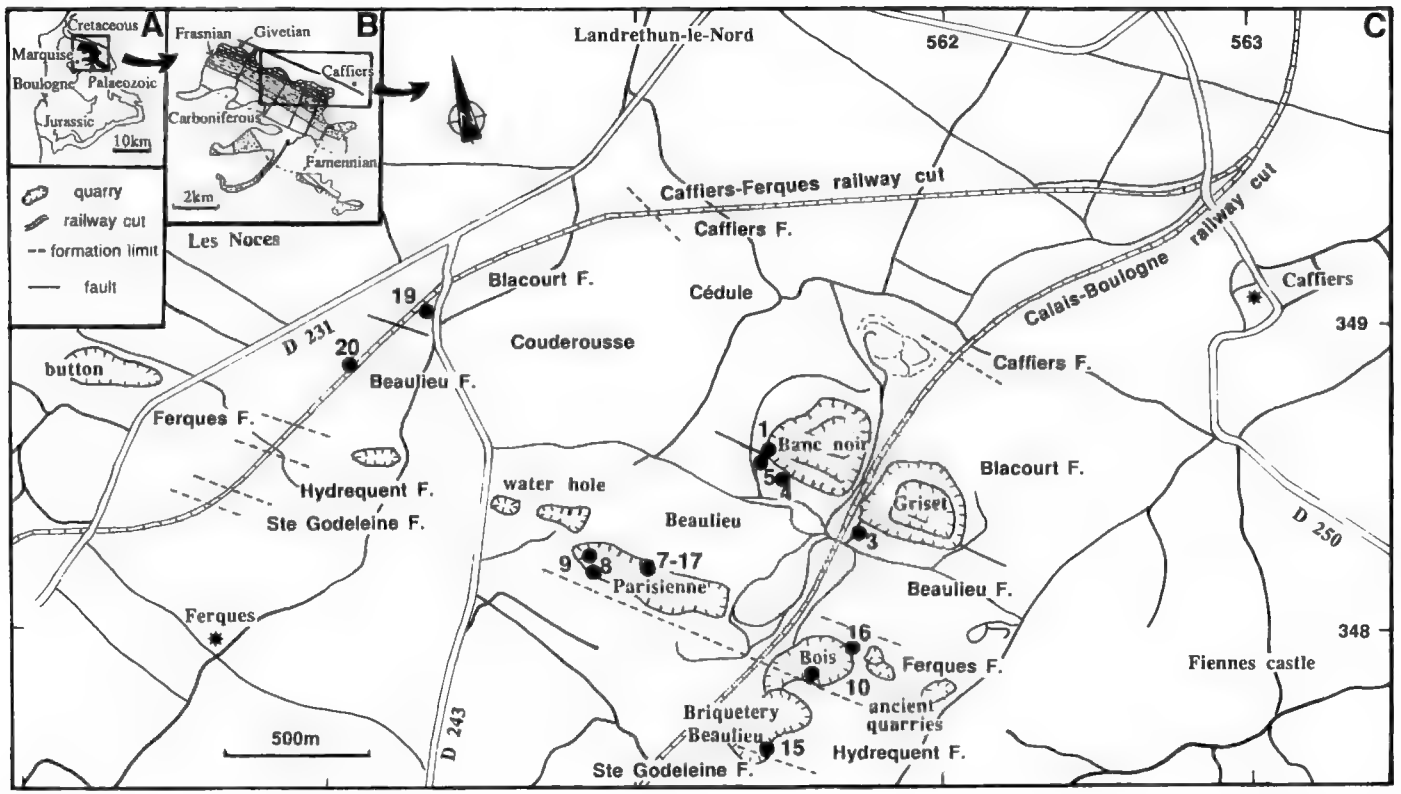

FIG. 2. — Location of samples after BRICE (1988a, b, c, Fig. 1 modified). A, Boulonnais. B, Palaeozoic inlier of Ferques. C, quarries and railway cuts with (1 to 20) location of samples BLN1 to BLN20.
Abbr.: F is for Formation.

Localisation des échantillons d'après BRICE (1988a, b, c, Fig. 1 modifiée). A, Boulonnais. B, massif paléozoïque de Ferques. C, carrières et tranchées de chemins de fer avec (1 à 20) localisation des échantillons BLN1 à BLN20. Abrév. : F correspond à Formation.

Upper part of the Ferques Formation (Gris Member or La Parisienne Member) at the bottom of La Parisienne quarry (BLN8, not *in situ*) and uppermost bed of the Bois quarry near the Briqueterie quarry (BLN10) (Frasnian, upper *P. asymmetricus* and *Ag. triangularis* zones).

HYDREQUENT FORMATION

Thick dolomitic bed, Briqueterie quarry (BLN15; Frasnian, *Ag. triangularis* zone). Another sample from this formation (H214; A. LEFRANÇOIS, pers. comm.) has yielded a few broken teeth.

Most samples were studied morphologically using a S.E.M. Cambridge Stereoscan 240; however, samples BLN19 and 3-4 were so rich in microremains that it was possible to make thin sections for histological study.

SYSTEMATICS

The new fossil assemblages discovered in Boulonnais are the first abundant records of fish microfaunas in the Devonian of France. They are composed of scales, teeth and lepidotrichia of gnathostomes, that is possible placoderms and numerous chondrichthyans, acanthodians and osteichthyans. no agnathan remains having been found. However, precise taxonomic determination to species rank is rarely possible and open nomenclature at the generic rank is employed.

As all higher groups of gnathostomes are concerned, we are faced with a huge problem of taxonomy and classification We thus decided to follow one recent consensus about the phylogenetic relationships of higher groups as exemplified by SCHULTZE (1990; Fig. 7), with the placoderms, chondrichthyans, acanthodians and osteichthyans as classes. For each class, we follow DENISON's (1978) classification of placoderms, ZANGERL's (1981) classification of chondrichthyans (slightly modified according to DERYCKE *et al.*, 1995), and DENISON's (1979) classification of acanthodians. Osteichthyans brought us a more difficult problem mainly because of the sarcopterygian phylogeny and classification which are not stabilized. A number of discussions occured in recent years on this matter without any consensus (see, e.g. FOREY, 1987; SCHULTZE, 1987, 1991; VOROBYEVA & SCHULTZE, 1991; FOREY *et al.*, 1991), except in the proposals of JANVIER (1986), AHLBERG (1991) and CLOUTIER (1991a-b) [see GEE, 1990]. So we refer to the latter.

Class PLACODERMI Mc Coy, 1848
Order PTYCTODONTIDA Gross, 1932
Family PTYCTODONTIDAE Woodward, 1891
Genus **RHYNCHODUS** Newberry, 1873

TYPE SPECIES. — *R. secans* Newberry, 1873; Middle Devonian (Eifelian), USA.

Rhynchodus? sp.
(Pl. II, B)

REFERRED MATERIAL. — CVUL 37 from BLN5.

DESCRIPTION

The specimen seems to be a lower left gnathal plate or inferognathal in which the shearing edge is worn and the lateral lamina is broken. It is comparable with the *Rhynchodus* sp. published by BELLES-ISLES *et al.* (1987) from the Givetian of Ferques. At first glance, the most evident difference is the length. The Frasnian inferognathal from BLN5 (Pl. II, B) is millimetric whereas the Givetian superognathal is centimetric. There is no groove visible in the lingual view which is just a progressive curvature of the lamina. It is the only recognized piece of Placodermi in our material. As often, the placoderms which are the dominant remains in fish macrofaunas for the Devonian both in number of genera and families (YOUNG, 1990; LONG, 1993) are not well represented in microremains.

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Order SYMMORIIDA Zangerl, 1981
Family SYMMORIIDAE Dean, 1909
Genus **SYMMORIUM** Cope, 1893

TYPE SPECIES. — *S. reniforme* Cope, 1893 (redescribed by WILLIAMS, 1985); Carboniferous, North America.

Symmorium? sp.
(Fig. 3a-b; Pl. I, D)

REFERRED MATERIAL. — CVUL 27 from BLN8.

DESCRIPTION AND DISCUSSION

The cladodont tooth CVUL 27 shows a kidney-shaped base with a slight concavity below the main cusp. This not well pronounced character permits us to compare our specimen to *Symmorium* (WILLIAMS, 1985: 103). A crown view shows the main broad cusp and the two pairs of lateral cusps settled along the labial margin of the base. The former one has an 8-sided section delimited by ridges on the surface; the labial flattened side and the lingual convex side are separated by a cutting edge. Contrary to the central cusp, the lateral ones have a labio-lingually directed greater length, with an elliptic shape in cross section. An aboral view shows a line of foramina in a depression parallel with the labial side (Fig. 3a). Some other little foramina are dispersed: three at the lingual margin of the base and two on the lingual face under the lateral cusps. A very extended boss exists lingually on the base (Fig. 3b). Its labial face is characterized by a concavity. It seems that the characters of *Symmorium* are in this specimen not so pronounced; for instance, the two facets described by ZIDEK (1992) as a character of *Symmorium* are not so evident here. This is the first occurence of a symmoriid at so early a level, the genus *Symmorium* having been described in the upper Famennian of northern Thailand (LONG, 1990), the Lower Carboniferous of North America (WILLIAMS, 1985; ZANGERL, 1981), Germany (MADER & SCHULTZE, 1987), France (DERYCKE *et al.*, 1995), and up to the late Pennsylvanian of New Mexico, USA (ZIDEK, 1992).

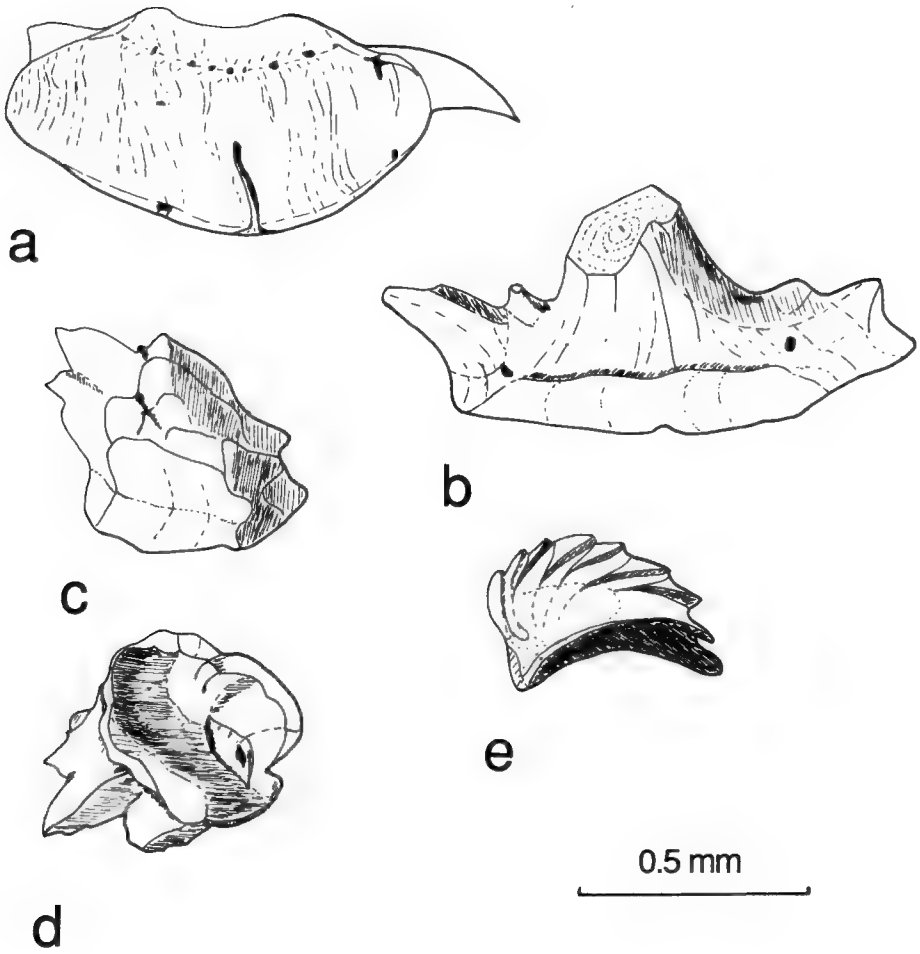

FIG. 3. — Chondrichthyan (a-d) and acanthodian (e) microremains from the Devonian of Bas-Boulonnais, France. a-b, *Symmorium?* sp., tooth CVUL 27 from BLN8, Ferques Formation, Frasnian, in aboral (a) and lingual (b) views, same as pl. I, d. c-d, *Chondrichthyes* gen. et sp. indet. Type A, denticle CVUL 24 from BLN4, Beaulieu Formation, Frasnian, in lateral (c) and aboral (d) views, same as pl. I, A; e, *Ptomacanthus?* sp., tooth-whorl CVUL 31 from BLN3, Beaulieu Formation, Frasnian, in lateral view, same as pl. I, H.

Microrestes de Chondrichthyens (a-d) et d'Acanthodiens (e) du Dévonien du Bas-Boulonnais, France. a-b Symmorium ? *sp., dent CVUL 27 de BLN8, Formation de Ferques, Frasnien, en vues aborale (ou basale, a) et linguale (b), même spécimen que pl. I, D. c-d,* Chondrichthyes *gen. et sp. indet. Type A, denticule CVUL 24 de BLN4, Formation de Beaulieu, Frasnien, en vues latérale (c) et aborale (ou basale, d), même spécimen que pl. I, A. e,* Ptomacanthus ? *sp., spirale dentaire CVUL 31 de BLN3, Formation de Beaulieu, Frasnien, en vue latérale, même spécimen que pl. I, H.*

Superorder EUSELACHII Hay, 1902
Order CTENACANTHIFORMES Nelson, 1976
Superfamily CTENACANTHOIDEA Dean, 1909
Family CTENACANTHIDAE Dean, 1909
Genus **CTENACANTHUS** Agassiz, 1835

TYPE SPECIES. — *Ctenacanthus major* Agassiz, 1835; Lower Carboniferous, England.

Ctenacanthus sp.
(Pl. I, B-C)

REFERRED MATERIAL. — CVUL 25 (Pl. I, B) and CVUL 26 (Pl. I, C) from BLN8.

DESCRIPTION

These two ctenacanthid scales *sensu* REIF (1978) present some common characteristics, that is a base separated from the crown by a gently pronounced neck and a convex crown towards the front. In CVUL 25 (Pl. I, B), six broad ridges separating deep grooves form the crown, whereas the crown of CVUL 26 (Pl. I, C) is made of three strong ridges. The surface of the broadest ridge (Pl. I, C) is traversed by a longitudinal groove in its basal part. The former scale (Pl. I, B) only has a forecrown whereas a notch exists in the middle of the labial basal rim of the latter (Pl. I, C).

CHONDRICHTHYES gen. et sp. indet.
Type A
(Fig. 3c-d; Pl. I, A)

REFERRED MATERIAL. — CVUL 24 from BLN4.

DESCRIPTION

This element presents a crown separated from the base by a little marked neck. The crown is made of little sharp spikes directed towards the rear of the animal (Fig. 3c). These spikes are smaller anteriorly and determine a polarity. The base shows a large concavity (Fig. 3d). This seems to be a chondrichthyan scale or perhaps a complex mucous membrane denticle with numerous cusps.

Type B
(Pl. I, E)

REFERRED MATERIAL. — CVUL 28 from BLN3.

DESCRIPTION

This specimen is composed of two rows of two imbricated teeth showing cutting edges. The two teeth in the foreground are not strictly in the same plane, they seem staggered and divergent. This composed element perhaps represents non-functional teeth.

Type C
(Pl. I, F)

REFERRED MATERIAL. — CVUL 29 from BLN3.

DESCRIPTION

The scale CVUL 29 has a centrifugal growth with smaller flat peaks in the centre. The scale has been growing in four directions but with different rates, and the more anterior part of the crown would be the left one on the SEM micrograph where two files do exist.

Type D
(Pl. I, G)

REFERRED MATERIAL. — CVUL 30 from BLN1.

DESCRIPTION

The microremain CVUL 30 is characterized by three bud-shaped cusps which constitute a high crown with a deeply grooved ornament drawing a circle-arch. The two external cusps show a pentameric symmetry whereas the less prominent central one has a tetrameric symmetry. The ornamentation is similar to that of *Arauzia federicoi* MADER (1986, Pl. 6, Fig. 6a) from the Lower Devonian of Spain.

Class ACANTHODII Owen, 1846
Order CLIMATIIDA Berg, 1940
Family CLIMATIIDAE Berg, 1940
Genus **PTOMACANTHUS** Miles, 1973

TYPE SPECIES. — *Ptomacanthus anglicus* Miles, 1973; Lower Devonian, England.

Ptomacanthus? sp.
(Fig. 3e; Pl. I, H)

REFERRED MATERIAL. — CVUL 31 from BLN3.

DESCRIPTION

This specimen seems to be an acanthodian tooth-whorl arranged in a single row. It is composed of six cusps with the smallest at the anterior part and covering the older just behind it (Fig. 3e). As in *Ptomacanthus*, the row is made of flat blade-like teeth (MILES, 1973). If it is a symphyseal tooth-whorl, the cusps should be directed posteriorly or lingually; it could be a pharyngeal tooth.

Order ACANTHODIDA Berg, 1940

Family ACANTHODIDAE Huxley, 1861
Genus **ACANTHODES** Agassiz, 1833

TYPE SPECIES. — *Acanthodes bronni* Agassiz, 1833; Lower Permian, Germany.

Acanthodes sp.

Type A
(Fig. 4; Pl. I, I, L)

REFERRED MATERIAL. — CVUL 32 (Pl. I, I) and CVUL 35 (Pl. I, L) from BLN19.

DESCRIPTION

In the sample BLN19, there are more than one hundred minute acanthodian body scales. They are typically rhomboidal with a flat smooth crown. A little concavity exists at the top of

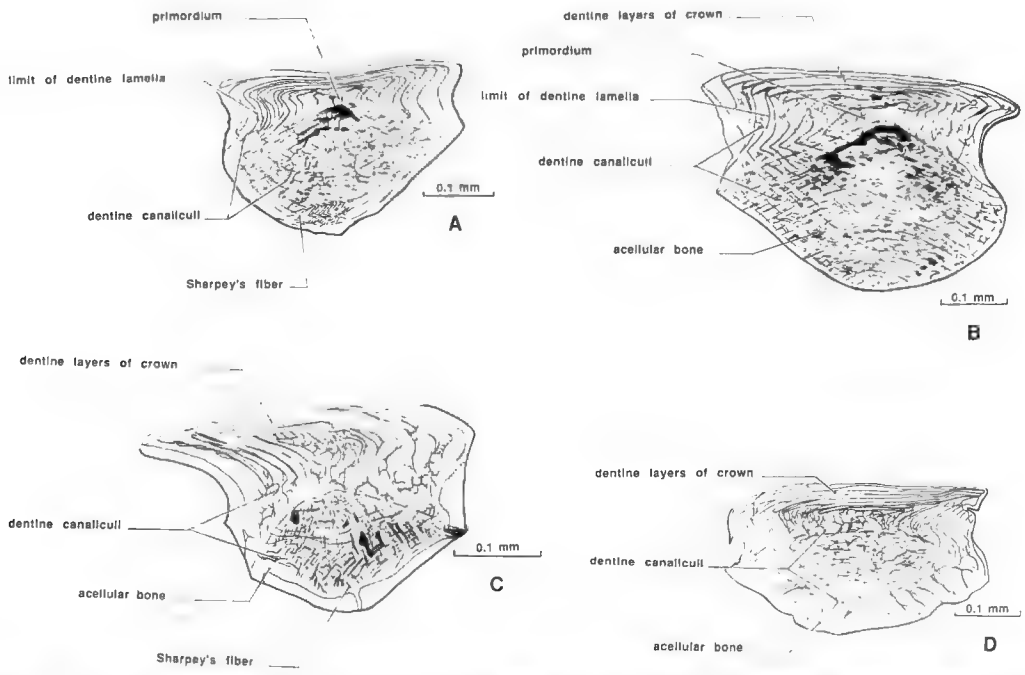

FIG. 4. — Histology of *Acanthodes* sp. Type A scales from BLN19 (Blacourt Formation, Couderousse Member, Upper Givetian). A-B, transverse thin sections. C-D, sagittal thin sections. The absence of cell-spaces confirms the *Acanthodes* type *sensu* GROSS (1947) and ØRVIG (1951). The well preserved structures show dentine canaliculi, Sharpey's fibers and growth concentric zones.

*Histologie d'écailles d'*Acanthodes *sp. Type A de BLN19 (Formation de Blacourt, Membre de Couderousse, Givétien supérieur). A-B, lames minces de coupes transversales. C-D, lames minces de coupes sagittales. L'absence d'espaces cellulaires confirme l'appartenance au type* Acanthodes *sensu* GROSS *(1947) et* ØRVIG *(1951). Les structures bien conservées montrent des canalicules de dentine, des fibres de Sharpey et des zones concentriques de croissance.*

the surface. Forwards, the crown is a little bit round and behind it forms an acute angle. The neck separating the convex base from the crown is narrow but well-defined.

HISTOLOGY

Thin sections through these scales corroborate the determination based on the morphology. As a matter of fact, the absence of cell-spaces (Fig. 4) confirms the *Acanthodes* type *sensu* GROSS (1947) and ØRVIG (1951). Moreover dentine canaliculi and Sharpey's fibers are visible in the base (compare to HEYLER, 1969). Transverse thin sections (Fig. 4A-B) show the continuous concentric zones in the crown and the base around the primordium (DENISON, 1979). The crown is made of concentric well drawn, true dentine layers. Those growth marks may illustrate rhythms of the animal.

DISCUSSION

The genus *Acanthodes*, generally recorded from Carboniferous and Permian levels, seems to be represented by Devonian species but they make a systematic problem. ZIDEK (1976) indeed considers *Acanthodes* as a *nomen dubium* while, for DENISON (1979), all the Devonian scales attributed to *Acanthodes* "are surely not *Acanthodes*" and, for WANG & TURNER (1985), "the whole family is in need of revision". We thus tentatively determine the new material from BLN19 as *Acanthodes* sp.

Type B
(Pl. I, J-K)

REFERRED MATERIAL. — CVUL 33 from BLN8 (Pl. I, J) and CVUL 34 from BLN17 (Pl. I, K).

DESCRIPTION

This typically rhombic-crowned scale has a clearly constricted neck. Forwards, the crown does not overhang the base and there is a gap between the crown and the base. Posteriorly, the crown presents a projection overlapping the base. As generally in the family Acanthodidae, the scale is smooth (DENISON, 1979).

Acanthodii gen. et sp. indet.
(Pl. II, A)

REFERRED MATERIAL. — CVUL 36 from BLN4.

DESCRIPTION

This tooth plate presents few rows of striated teeth. Each tooth is orientated lingually and presents a wide pulp cavity. The labial row consists of seven teeth which are more acute in the middle part. A bigger cusp, located at the left in the second plane of the SEM micrograph (Pl. II, A), had existed but is broken.

Class OSTEICHTHYES Huxley, 1880
Subclass ACTINOPTERYGII Klein, 1885

In our samples, numerous actinopterygian microremains have been prepared from BLN4 and BLN3, in the Beaulieu Formation, and some others from BLN8-10 and 16-17 in the Ferques Formation (Fig. 5). They comprise flank scales, ventral scales and scales from the upper part of the tail of the types previously detailed by JESSEN (1968). Our material is not particularly well preserved but, as LONG (1988) already noticed, "in the world few Devonian actinopterygians are well-known". So any new record has to be mentioned. *Osorioichthys* CASIER (1952, 1954) was the first actinopterygian to be described from the Late Devonian of Belgium and, later, LELIÈVRE *et al.* (1988) figured few microremains from the Givetian of Boulonnais. They were all attributed to palaeoniscoid taxa.

This point needs a short comment. Among actinopterygians, LEHMAN (1966) considers that "Chondrostei" do not really exist and GARDINER (1967) thinks that "the Chondrostei, the Holostei, the Halecostomi and the Teleostei... represent grades of evolutionary development rather than natural subdivisions" (see also LAUDER & LIEM, 1983). In their classifications, Palaeoniscoidei are thus considered as a paraphyletic group (GARDINER, 1984, 1986). Our specimens are identified at the generic level only or are considered undetermined, and do not allow a review of the "palaeoniscoids". So we provisionally use GARDINER's (1967) classification. Our material is represented, as all actinopterygians, by ganoid-type scales with three superposed layers: a ganoin external one above dentine and bony layers (see LEHMAN, 1966). The onion-skin growth of the ganoin is visible on some of the thin sections (Fig. 5B). The base of the scales is made of bone with many cell spaces and Sharpey's fibers for attachment (Fig. 5A-D). The crown is thin with regard to the bony base. The hemilepidotrichium fin-ray has a pyramidal section (Fig. 5E).

Order "PALAEONISCIFORMES"
Suborder "PALAEONISCOIDEI"
Family STEGOTRACHELIDAE Gardiner, 1963
Genus **MOYTHOMASIA** Gross, 1950

TYPE SPECIES. — *Moythomasia perforata* Gross, 1950; Upper Devonian (Frasnian), Germany and Western Australia.

Moythomasia sp.
(Pl. II, C-E)

REFERRED MATERIAL. — CVUL 38 from BLN8 (Pl. II, C), CVUL 39 from BLN3 (Pl. II, D) and CVUL 40 from BLN4 (Pl. II, E).

DESCRIPTION

The scale CVUL 38 (Pl. II, C) shows the peg and socket articulation between scales which is characteristic of advanced actinopterygians. The peg (which faces right on Pl. II, C) is a dorsal process and the smooth overlap surface (which faces up) is frontal. So we can orientate

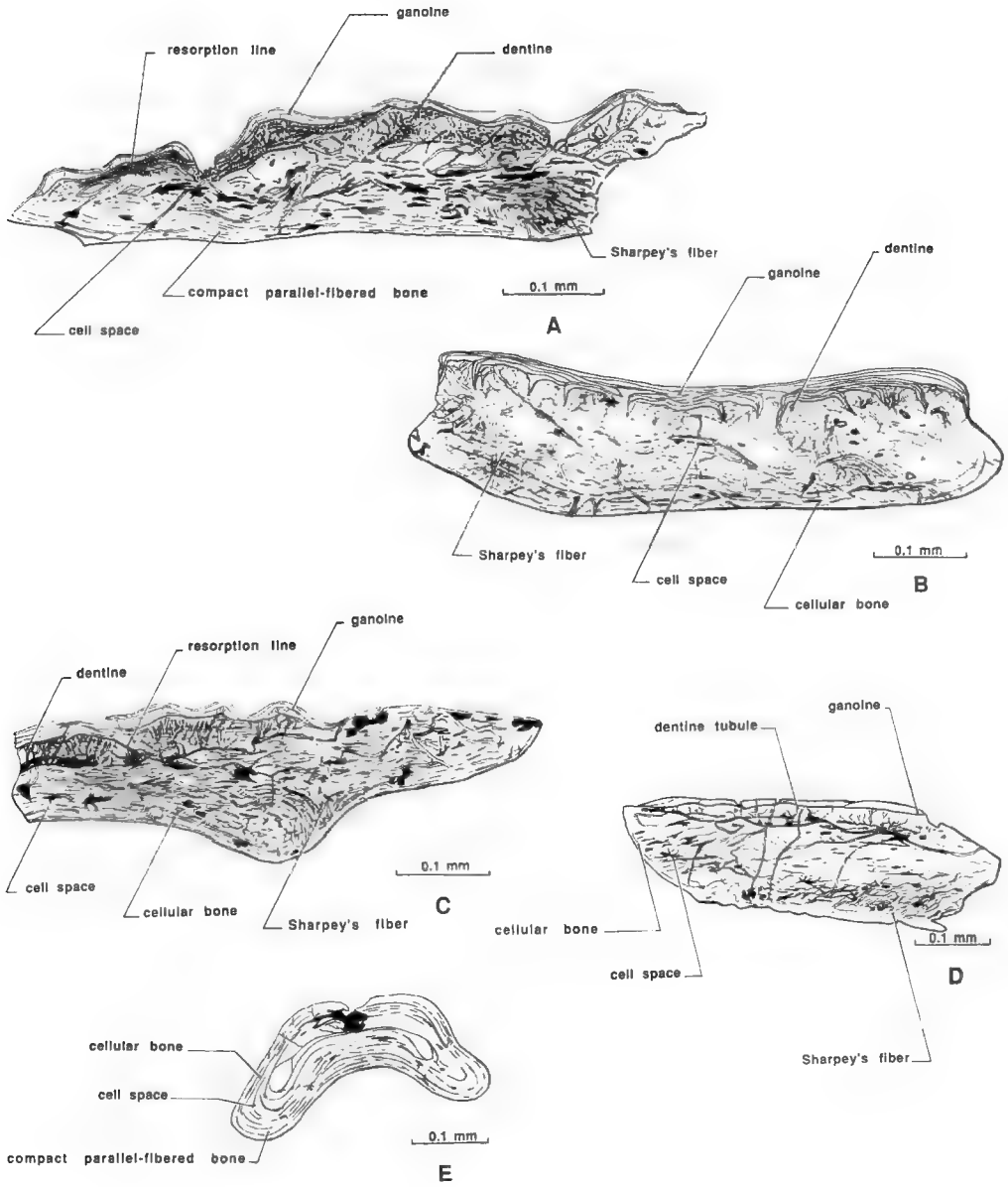

FIG. 5. — Histology of undetermined actinopterygian microremains from BLN4 and 3 (Beaulieu Formation, Cambreseque Member, Frasnian). A-D, thin sections of scales from BLN3. E, thin section of a hemilepidotrichium from BLN4.

Histologie de microrestes d'Actinoptérygiens indéterminés de BLN4 et 3 (Formation de Beaulieu, Membre de Cambresèque, Frasnien). A-D, lames minces d'écailles de BLN3. E, lame mince d'un hémilépidotriche de BLN4.

this microremain as a left flank scale. The antero-ventral angle equals about 135°. The surface is worn but we can see ripples of ganoin. This diamond-shaped scale comes probably from the ventro-lateral flank of the animal. One rectangular scale (Pl. II, D) is ornamented by a layer of perforated ganoin whose pores are aligned in curve directions. Its posterior margin is serrated with three denticulations in the prolongation of the direction of its diagonal axis. It seems to represent a right flank scale on which we can define an antero-ventral angle between the overlap anterior surface (which faces right on Pl. II, D) and the ventral margin (which faces down) opposite the peg. This antero-ventral angle is obtuse (125°). The shape of the third figured scale CVUL 40 recalls a ventral scale. Its anterior part, which represents the overlap area, faces left on Pl. II, E. The antero-ventral angle is approximately 77°. Such an acute angle is also found in the ventral scales of *Howqualepis* (LONG, 1988, Fig. 26). The anterior and dorsal margin of the shiny part is finely striated. An oblique line of pores crosses the exposed surface.

Actinopterygii gen. et sp. indet. AB
Type A
(Pl. II, F)

REFERRED MATERIAL. — CVUL 41 from BLN5.

DESCRIPTION

A tooth plate CVUL 41 (Pl. II, F) is composed of more than twenty cusps. Each cusp is ornamented with dashed cristae; SCHULTZE (1977) interpreted this structure as ganoin. Two of them exhibit an acrodin cap. All cusps are gently constricted around their point of insertion.

Type B
(Pl. II, G)

REFERRED MATERIAL. — CVUL 42 from BLN8.

DESCRIPTION

The tooth CVUL 42 (Pl. II, G) is slightly curved with a tip of acrodin. Dashed cristations, the ornamentation of ganoin (SCHULTZE, 1977), are converging at the top of the tooth and some diverge from the lingual part towards the labial face. A large pulp cavity is noticeable at the base.

Type C
(Pl. II, I)

REFERRED MATERIAL. — CVUL 44 from BLN5.

DESCRIPTION

The absence of ganoin cover in CVUL 44 is surprising. However, it seems to be an actinopterygian left flank scale because of its rhombic shape and the presence of three serrations

at its posterior margin (which faces up on Pl. II, I). The ornamentation is peculiar with five parallel broken lines of pores, and, in the middle, two triangles of the cover butting into the transverse ridges.

Type D
(Pl. II, K)

REFERRED MATERIAL. — CVUL 46 from BLN3.

DESCRIPTION

The microremain CVUL 46 is divided into two parts. Its anterior one is shiny and covered by finely striated ganoin whereas the posterior one is bony. This element seems to correspond to a fin ray like those which have been interpreted as dorsal fin rays by SCHULTZE & BARDACK (1987, Fig. 13A). It also corresponds to half a lepidotrichium, the latter consisting of two opposite elements placed like parentheses; so this is a hemilepidotrichium. As on the most proximal lepidotrichia of brachyopterygians (Polypteridae) and of Lepisosteidae, an incomplete ganoin cover is found on CVUL 46 (Pl. II, K, refs in FRANCILLON-VIEILLOT *et al.*, 1990).

Subclass SARCOPTERYGII Romer, 1955
Order ONYCHODONTIDA Andrews, 1973
ONYCHODONTIDA gen. et sp. indet.
(Pl. II, L)

REFERRED MATERIAL. — CVUL 47 from BLN4.

DESCRIPTION

This specimen is a portion of the external face of the anterior covered part of a scale. It bears typical horse-shoe-shaped tubercles. This ornamentation is found in holoptychiids and onychodontids. The convexity of the tubercles indicates the posterior part of the animal (it faces up on Pl. II, L). Their base is oval and their top surface is sharply concave and spoon-like. The tubercle surface is shiny and probably formed of enamel. When compared to onychodontids, the ornamentation of CVUL47 differs from that of *Holoptychius*. On *Glyptolepis*, the tubercles seem more acute. However, it is suggestive of *Onychodus* (ØRVIG, 1957), a genus already represented by teeth in Boulonnais (LELIÈVRE *et al.*, 1988). A similar ornamentation occurs in *Grossius aragonensis* SCHULTZE (1973, Pl. 33) and *Heimenia ensis* ØRVIG (1969, Fig. 6). Two generations of tubercles are in fact represented on CVUL 47: one central line of three, a little taller and wider tubercles, flanked by lateral, more irregular lines. Diagonal alignments seem to be superimposed to that pattern. Another unfigured fragment of scale, with the same tuberculate ornamentation, also shows sinuous ridges. However, a comparable ornamentation has recently been described by SCHULTZE (1992) on scales of a dipnoan species, and it seems that spoon-like tubercles are a plesiomorphic character for Sarcopterygii (CLOUTIER, pers. comm.).

Order POROLEPIFORMES Jarvik, 1942
POROLEPIFORMES gen. et sp. indet.
(Pl. II, J, M)

REFERRED MATERIAL. — CVUL 45 (Pl. II, J) and CVUL 48 (Pl. II, M) from BLN4.

DESCRIPTION

The fragmentary specimen CVUL 48 is characterized by well marked sinuous and approximately parallel branching ridges. It resembles the external view of scales figured by JARVIK (1949: Pl. 8, 1) who compared them with scales of *Glyptolepis*. The piece of bone CVUL 45 (Pl. II, J) shows no evident organization but the general pattern of its ridges and intermediate pores look like that of CVUL 48 and both fragments are attributed to Porolepiformes (cf. ØRVIG, 1957; JARVIK, 1985).

Order RHIZODONTIDA Andrews & Westoll, 1970
Family RHIZODONTIDAE Traquair, 1881
Genus **SPODICHTHYS** Jarvik, 1985

TYPE SPECIES. — *Spodichthys buetleri* Jarvik, 1985; Middle-Upper Devonian, Greenland.

Spodichthys? sp.
(Pl. II, H)

REFERRED MATERIAL. — CVUL 43 from BLN4.

DESCRIPTION

On this fragment of bone, horizontal ridges are connected by short regularly spaced cross ridges. They form alignments of rectangles or lozenges.This specimen reminds us of scales published by JARVIK (1985, Fig. 35).

SUMMARY AND CONCLUSIONS

This is a preliminary report of new microvertebrate material from the upper Middle-lower Upper Devonian of northern France. Part of the samples is presented, the rest being treated in a Ph. D. thesis defended by one of us (C. D.). As vertebrate microremains have been proved useful in biostratigraphy, one of the aims of this work is to settle their stratigraphical ranges in the Palaeozoic orogen of northern France-southern Belgium. However, only a few of the ichthyoliths figured here can be placed in settled taxonomic groups, so this paper may raise more problems than it solves. LELIÈVRE *et al.* (1988) have mainly studied the macrofauna of the

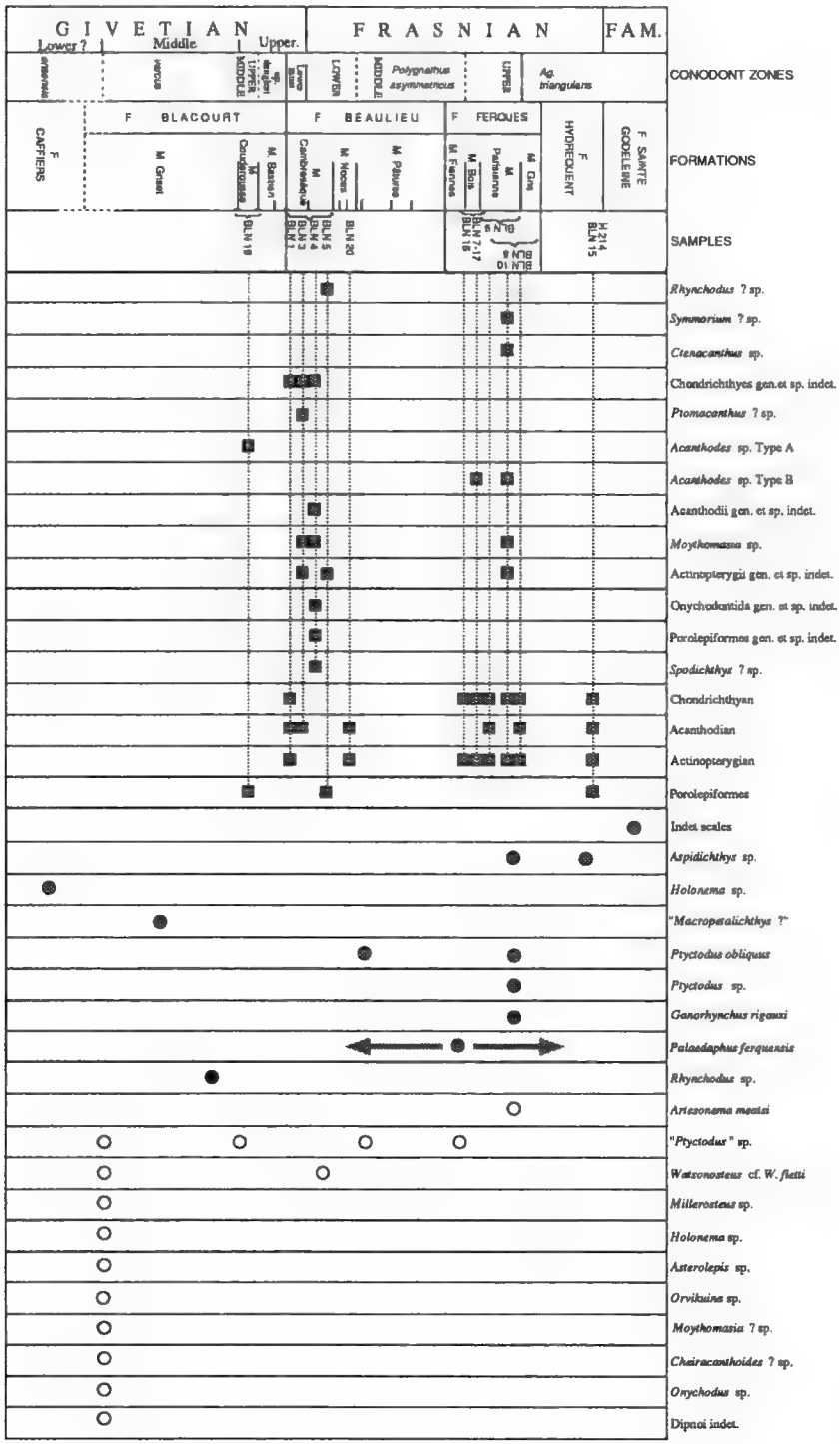

FIG. 6. — Compiled stratigraphical distribution of the Devonian vertebrates of Boulonnais. The different points indicate the stratigraphical location of the specimens figured by DUTERTRE (1930, grey circles), BELLES-ILES *et al.* (1987, black circles) and LELIÈVRE *et al.* (1988, white circles); some of the stratigraphical levels are uncertain. Our reported material: grey squares.

Distribution stratigraphique synthétique des Vertébrés du Dévonien du Boulonnais. Les différents points indiquent la localisation stratigraphique des spécimens figurés par DUTERTRE *(1930, cercles gris),* BELLES-ILES et al. *(1987, cercles noirs) et* LELIÈVRE et al. *(1988, cercles blancs). Quelques localisations stratigraphiques sont incertaines. Le matériel que nous décrivons ici correspond aux carrés gris.*

Givetian-Frasnian of Boulonnais with just a few microremains from the Givetian lower Blacourt Formation. Here uppermost Givetian-Frasnian microfaunas are outlined. Acanthodians, chondrichthyans, actinopterygians and sarcopterygians are well represented, the placoderms are very rare. Some rock samples are particularly rich in ichthyoliths as BLN19 (uppermost Givetian, upper Blacourt Formation) which yielded a mass of acanthodian scales, or BLN3 and BLN4 (lowermost Frasnian, lower Beaulieu Formation) which gave numerous actinopterygian scales. We also show the first occurrence of Palaeozoic chondrichthyans in Boulonnais. Among them, the presence of Symmoriidae is one of the oldest recorded examples of this family.

Among acanthodians, the *Acanthodes* type has been recognized in thin sections; however, the taxonomic attribution of this material has to be revised because the Devonian "*Acanthodes*" seem to differ from the genus as defined in younger levels. One evidence only of the presence of Placodermi has been found, *i.e.* an inferognathal belonging to the Ptyctodontidae. In our samples, the actinopterygians are the second group well represented in number of microremains, with scales of *Moythomasia*. This genus has been many times described in the Upper Devonian of Germany (GROSS, 1950; JESSEN, 1968) and of Australia (GARDINER, 1984). The other actinopterygian scales, considered undetermined, have no ganoin cover, which is surprising because classically ganoin ridges intercalated with bony grooves characterize Lower Devonian actinopterygians (SCHULTZE, 1968, 1977), although younger actinopterygian scales have a continuous ganoin cover (JANVIER & DE MELO, 1987). Among sarcopterygians, the Porolepiformes are compared with genera from the Middle Devonian of Norway, the Frasnian of Quebec and the Middle-Upper Devonian of Greenland (JARVIK, 1949, 1985; ØRVIG, 1957).

In conclusion, we give a compiled stratigraphical distribution of all previous records of Devonian fishes in the Boulonnais, including the new ones (Fig. 6). It shows clearly that few levels have a diversified fauna:

1) one in the Givetian lower Blacourt Formation (LELIÈVRE *et al.*, 1988) in which placoderms are predominant;

2) samples from the lower Frasnian, lower Beaulieu Formation (this record) in which all gnathostome higher taxa are represented (from placoderms to sarcopterygians);

3) samples in the Frasnian Ferques Formation (this record) with mainly chondrichthyans and actinopterygians. The marine nature of all these levels is undeniable by the occurrence of a large array of invertebrates (BRICE, 1988b).

When compared to approximately contemporary ichthyofaunas, different conclusions are drawn. The Givetian fauna of the Blacourt Formation is close to those from Scotland and the Baltic (LELIÈVRE *et al.*, 1988). On the contrary, the lower Frasnian fauna of the Beaulieu Formation has no vertebrate element in common with, for example, the fauna of the Escuminac Formation of Quebec (see, e.g. SCHULTZE & CLOUTIER, 1991). This difference may be owing to taphonomical conditions and sampling bias (with mainly microremains in Boulonnais and macrofaunas in Quebec), or to environmental differences (with less saline conditions in Quebec), or both. These conclusions are thus in disagreement with the classical view of cosmopolitan Late Devonian faunas (YOUNG, 1987). They are also in disagreement with the conclusions of BRICE (1988a-b) who has shown that some genera of tabulate corals, brachiopods, echinoids, ostracodes of Boulonnais are related to or close to North American ones, implying marine communications between both areas. The European taxa being stratigraphically younger than the

North American ones, this also leads to hypothesize migrations from west to east, which cannot be concluded from the microvertebrate faunas.

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PLATE I. — Chondrichthyan and acanthodian microremains from the Devonian of Bas-Boulonnais, France. All scale-bars equal 200 µm. A, *Chondrichthyes* gen. et sp. indet. Type A. Denticle CVUL 24 from BLN4, Beaulieu Formation, Frasnian, crown view. The crown cusps are directed towards the rear of the animal and face left. B-C, *Ctenacanthus* sp. Scales CVUL 25 (B) and CVUL 26 (C) from BLN8, Ferques Formation, Frasnian, crown (B) and front (C) views. The convex sides indicate the front directions which face down. D, *Symmorium* ? sp. Tooth CVUL 27 from BLN8, Ferques Formation, Frasnian, occlusal view. The lingual side is indicated by the concavity of the cusps and faces down. E, *Chondrichthyes* gen. et sp. indet. Type B. Imbricated teeth CVUL 28 from BLN3, Beaulieu Formation, Frasnian, lingual view. F, *Chondrichthyes* gen. et sp. indet. Type C. Scale CVUL 29 from BLN3, Beaulieu Formation, Frasnian, crown view. G, *Chondrichthyes* gen. et sp. indet. Type D. Scale CVUL 30 from BLN1, Beaulieu Formation, La Cedule limestone, upper Givetian, crown view. H, *Ptomacanthus?* sp. Tooth-whorl CVUL 31 from BLN3, Beaulieu Formation, Frasnian, crown view. I, L, *Acanthodes* sp. Type A. Typical rhomboidal scales with flat smooth crowns CVUL 32 (I) and CVUL 35 (L) from BLN19, Blacourt Formation, Upper Givetian, basal (I) and crown (L) views. J, K, *Acanthodes* sp. Type B. Scales with higher neck CVUL 33 (J) from BLN8 and CVUL 34 (K) from BLN17, Ferques Formation, Frasnian, frontal (J) and latero-frontal (K) views.

Microrestes de chondrichthyens et d'acanthodiens du Dévonien du Bas-Boulonnais, France. Toutes les échelles métriques correspondent à 200 µm. A, Chondrichthyes *gen. et sp. indet. Type A. Denticule CVUL 24 de BLN4, Formation de Beaulieu, Frasnien, vue coronale. Les cuspides de la couronne sont dirigées vers la partie postérieure de l'animal, vers la gauche. B-C,* Ctenacanthus *sp. Ecailles CVUL 25 (B) and CVUL 26 (C) de BLN8, Formation de Ferques, Frasnien, vues coronale (B) et frontale (C). Les côtés convexes indiquent les faces antérieures qui sont dirigées vers le bas. D,* Symmorium ? *sp. Dent CVUL 27 de BLN8, Formation de Ferques, Frasnien, vue occlusale. Le côté lingual est indiqué par la concavité des cuspides, orientée vers le bas. E,* Chondrichthyes *gen. et sp. indet. Type B. Dents imbriquées CVUL 28 de BLN3, Formation de Beaulieu, Frasnien, vue linguale. F,* Chondrichthyes *gen. et sp. indet. Type C. Ecaille CVUL 29 de BLN3, Formation de Beaulieu, Frasnien, vue coronale. G,* Chondrichthyes *gen. et sp. indet. Type D. Ecaille CVUL 30 de BLN1, Formation de Beaulieu, calcaire de la Cédule, Givétien supérieur, vue coronale. H,* Ptomacanthus ? *sp. spirale dentaire CVUL 31 de BLN3, Formation de Beaulieu, Frasnien, vue coronale. I, L,* Acanthodes *sp. Type A. Écailles rhombiques typiques à couronnes lisses et plates CVUL 32 (I) et CVUL 35 (L) de BLN19, Formation de Blacourt, Givétien supérieur, vues basale (I) et coronale (L). J, K,* Acanthodes *sp. Type B. Écailles à collet plus haut CVUL 33 (J) de BLN8 et CVUL 34 (K) de BLN17, Formation de Ferques, Frasnien, vues frontale (J) et latéro-frontale (K).*

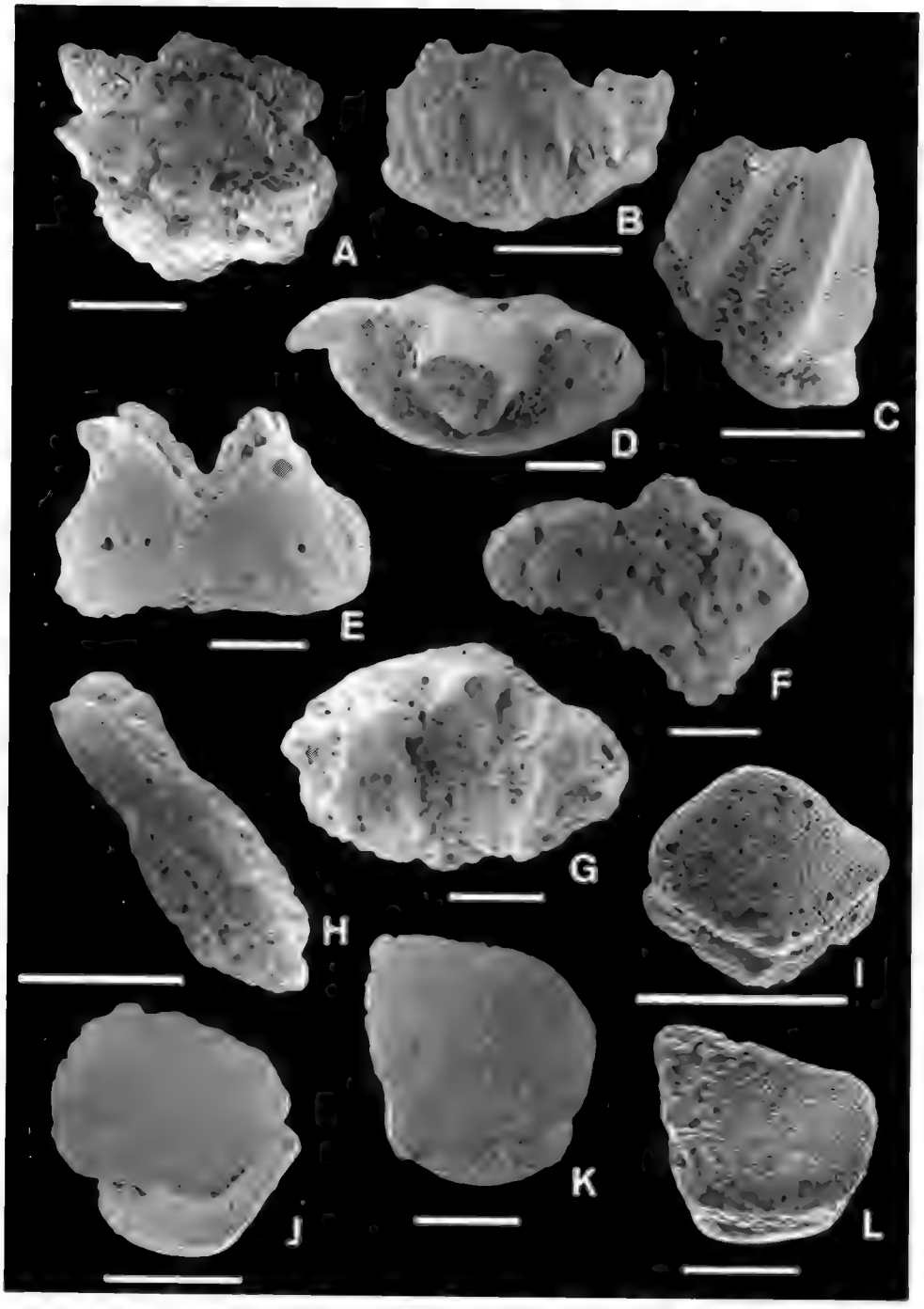
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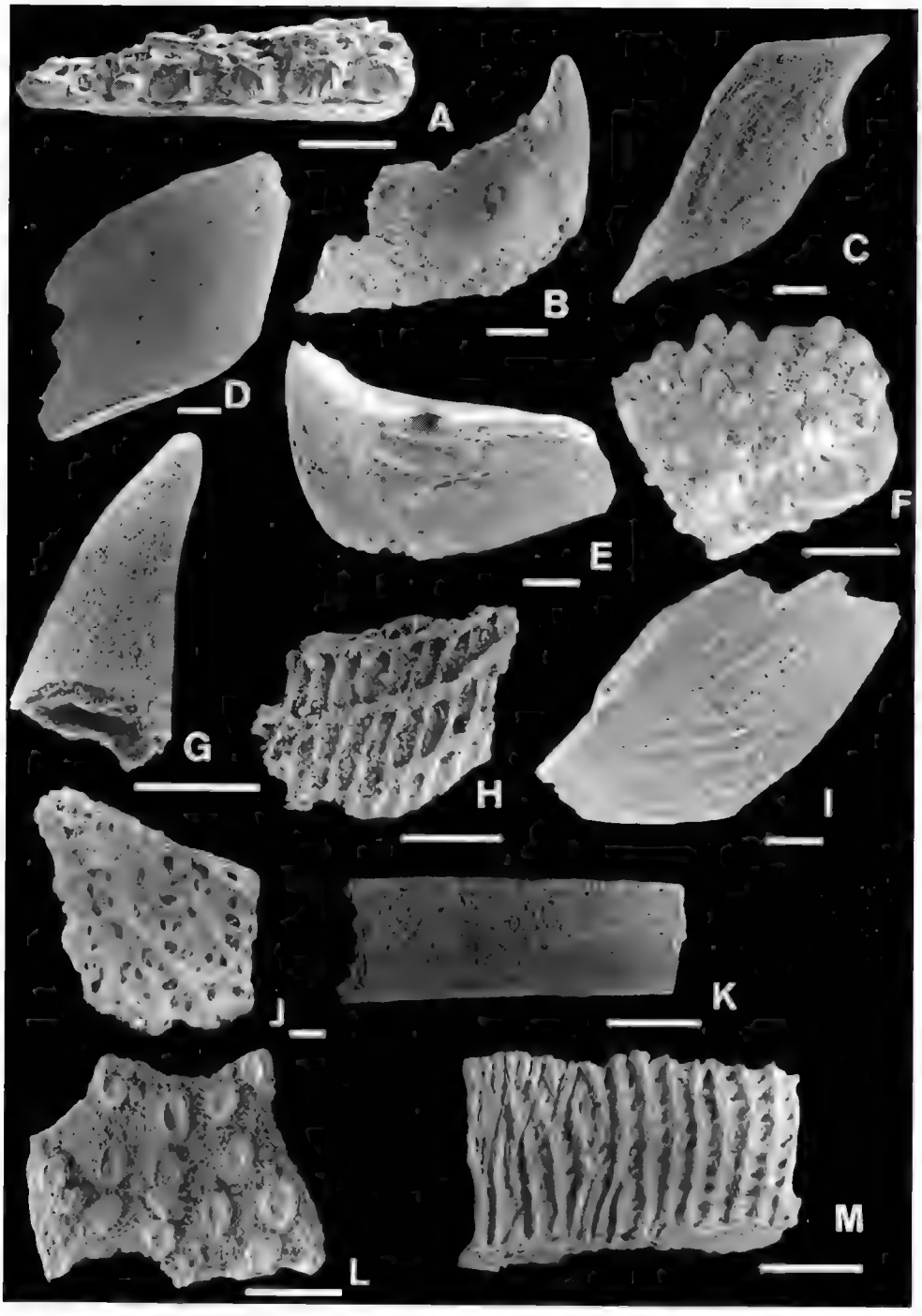
PLATE II. — Acanthodian, placoderm and osteichthyan microremains from the Devonian of Bas-Boulonnais, France. All scale-bars equal 200 µm. A, Acanthodii gen. et sp. indet. Tooth Plate with few rows of striated teeth CVUL 36 from BLN4, Beaulieu Formation, Frasnian, labial view. B, *Rhynchodus?* sp. Inferognathal CVUL 37 from BLN5, Beaulieu Formation, Frasnian, lingual view. C-E, *Moythomasia* sp. Scales CVUL 38 from BLN8 (C), Ferques Formation, CVUL 39 from BLN3 (D), and CVUL 40 from BLN4 (E), Beaulieu Formation, Frasnian. The front of the scale CVUL 38 (C) faces up and its dorsal side faces right. The front and the dorsal sides of CVUL 39 (D) face right and up respectively. The front of CVUL 40 (E) faces left and its dorsal side up. F, Actinopterygii gen. et sp. indet. Type A. Tooth Plate CVUL 41 from BLN5, Beaulieu Formation, lower Frasnian. G, Actinopterygii gen. et sp. indet. Type B. Tooth CVUL 42 from BLN8, Ferques Formation, Frasnian. H, *Spodichthys?* sp. Scale CVUL 43 from BLN4, Beaulieu Formation, Frasnian. I, Actinopterygii gen. et sp. indet. Type C. Scale CVUL 44 from BLN5, Beaulieu Formation, lower Frasnian. J, M, Porolepiformes gen. et sp. indet. fragments of bone CVUL 45 (J) and CVUL 48 (M) from BLN4, Beaulieu Formation, Frasnian. K, Actinopterygii gen. et sp. indet. Type D. Hemilepidotrichium CVUL 46 from BLN3, Beaulieu Formation, Frasnian. The covered part of the hemilepidotrichium faces down. L, Onychodontida gen. et sp. indet. Scale CVUL 47 from BLN4, Beaulieu Formation, Frasnian.

Microrestes d'Acanthodiens, de Placodermes et d'Ostéichthyens du Dévonien du Bas-Boulonnais, France. Toutes les échelles métriques correspondent à 200 µm. A, Acanthodii gen. et sp. indet. Os avec quelques rangées de dents striées CVUL 36 de BLN4, Formation de Beaulieu, Frasnien, vue labiale. B, Rhynchodus ? *sp. Inférognathal CVUL 37 de BLN5, Formation de Beaulieu, Frasnien, vue linguale. C-E,* Moythomasia *sp. Écailles CVUL 38 de BLN8 (C), Formation de Ferques, CVUL 39 de BLN3 (D), et CVUL 40 de BLN4 (E), Formation de Beaulieu, Frasnien. La partie antérieure de l'écaille CVUL 38 (C) est tournée vers le haut et son côté dorsal est orienté vers la droite. L'avant et la partie dorsale de CVUL 39 (D) sont tournés vers la droite et le haut respectivement. La partie antérieure de CVUL 40 (E) est tournée vers la gauche et son côté dorsal vers le haut. F, Actinopterygii gen. et sp. indet. Type A. Plaque denticulée CVUL 41 de BLN5, Formation de Beaulieu, Frasnien inférieur. G, Actinopterygii gen. et sp. indet. Type B. Dent CVUL 42 de BLN8, Formation de Ferques, Frasnien. H,* Spodichthys? *sp. Écaille CVUL 43 de BLN4, Formation de Beaulieu, Frasnien. I, Actinopterygii gen. et sp. indet. Type C. Écaille CVUL 44 de BLN5, Formation de Beaulieu, Frasnien inférieur. J, M, Porolépiformes gen. et sp. indet. Fragments d'os CVUL 45 (J) et CVUL 48 (M) de BLN4, Formation de Beaulieu, Frasnien. K, Actinopterygii gen. et sp. indet. Type D. Hémilépidotriche CVUL 46 de BLN3, Formation de Beaulieu, Frasnien. La partie recouverte de l'hémilépidotriche est tournée vers le bas. L, Onychodontida gen. et sp. indet. Écaille CVUL 47 de BLN4, Formation de Beaulieu, Frasnien.*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Early Silurian microvertebrates of eastern Canada

by Susan TURNER and Godfrey S. NOWLAN
(Contribution to IGCP 328 "Paleozoic Microvertebrates")

Abstract. — Early to Late Llandovery platformal strata from the Clemville, Weir, Anse aux Gascons, and Anse à Pierre-Loiselle Formations, Chaleurs Bay, Gaspé Peninsula, Quebec; Armstrong Brook and Limestone Point formations of northern New Brunswick; and limestone blocks from a fault zone at School Brook Cove, Nova Scotia, have yielded vertebrate microfossils associated with conodonts. Scales of loganiid thelodonts are relatively common comprising *Loganellia scotica* type, *Loganellia* sp. cf. *L. sibirica*, as well as a new form, a possible katoporid, *Valvalepis crista* n. g., n. sp. The latter is restricted to the lower Llandovery Clemville Formation. Rare scales resembling those of *Helenolepis* Karatajute-Talimaa, 1978 are present. Other scales and ornamented bones or platelets might be derived from chondrichthyans, an anaspid, or a gnathostome, either acanthodian or placoderm. The new assemblages share a close resemblance with those of the Late Ordovician and Llandovery of Timan-Pechora and Siberia and have features in common with faunas from the Llandovery elsewhere in Greenland, Britain, the Baltic and Tuva.

Keywords. — Vertebrata, Agnatha, Thelodonti, Silurian, Canada, systematics, biostratigraphy.

Microvertébrés du Silurien inférieur du Canada oriental

Résumé. — Des microrestes de Vertébrés associés à des Conodontes ont été extraits de séquences marines de plateforme du Llandovery inférieur à supérieur des formations de Clemville, Weir, Anse aux Gascons et Anse à Pierre-Loiselle, dans la Baie des Chaleurs, Gaspésie, Québec; des formations de Armstrong Brook et de Limestone Point du nord du Nouveau-Brunswick; et des blocs calcaires de la zone faillée de School Brook Cove, Nouvelle-Écosse. Les écailles de Thélodontes loganiides sont assez communes, avec les espèces *Loganellia scotica* et *Loganellia* sp. cf. *L. sibirica*, ainsi qu'un possible katoporide nouveau, *Valvalepis crista*. Cette dernière espèce est restreinte à la formation de Clemville (Llandovery inférieur). De rares écailles ressemblant à celles d'*Helenolepis* Karatajute-Talimaa, 1978 sont présentes. D'autres écailles ainsi que des os ornementés et de petites plaques osseuses semblent correspondre à un Chondrichthyen, un Anaspide ou un Gnathostome (Acanthodien ou Placoderme). Les nouveaux assemblages sont très proches de ceux de l'Ordovicien supérieur et du Llandovery de Timan-Pechora et de Sibérie, et ont des formes en commun avec les faunes du Llandovery du Groenland, de Grande-Bretagne, des Pays Baltes et de Tuva.

Mots-clés. — Vertebrata, Agnatha, Thelodonti, Silurien, Canada, systématique, biostratigraphie.

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INTRODUCTION

Vertebrate remains have been known from the Silurian of eastern Canada for some time. Isolated occurrences of thelodont scales in the Silurian of eastern Canada have been reported during this century (GARDINER, 1966; TURNER, 1976; BLIECK & JANVIER, 1991). Most of those

cited along with some of the new Lower Silurian material discussed here come from the Mascarene and Arisaig zones (WILLIAMS, in press) in the complex Appalachian orogenic belt of eastern North America. New Lower Silurian material here described from Quebec is from the Chaleur zone (WILLIAMS, op. cit.) and material from the Ludlow-Pridoli rocks of Newfoundland (FÅHRAEUS in BLIECK & JANVIER, 1991) comes from the Clam Bank zone (WILLIAMS, op. cit.). Thelodont scales have also been reported, but not yet verified, from the important key Lower Silurian succession of Anticosti Island (S. POHLER & C. BARNES, pers. comm. 1991).

In 1928 STETSON described new articulated thelodont material from New Brunswick as *Thelodus "macintoshi"*. Re-examination of these specimens by TURNER (1984, 1986) indicated that this material included large individuals of *Thelodus parvidens* as well as a loganellid and an acanthodian. The Early Silurian (late Llandovery) age of the fish-bearing beds in the Long Reach Formation is still disputed but there is little doubt that the beds are pre-Ludlow in age (TURNER, 1986; in press).

The Late Silurian to Early Devonian succession in the Arisaig zone of Nova Scotia is particularly rich in vertebrate remains that are closely related or identical to those in the Welsh Borderland, suggesting close proximity of these areas at the time (e.g. TURNER, 1970; BLIECK & JANVIER, 1991). ØRVIG seems to have examined the first thelodonts to be found in the Arisaig succession (in BOUCOT *et al.*, 1974). He identified thelodontidid scales of "*Thelodus parvidens* kind" associated with *Nostolepis* and *Gomphonchus* acanthodian scales and spines. BOUCOT *et al.* (1974) used the evidence of the fish fauna to give an Upper Silurian (Ludlow) date to the upper part of the Moydart Formation. We have not yet seen this material, but from what is already known of the range of *Thelodus parvidens* in the eastern Canada-western European region, the age of the Moydart could be as old as Wenlock and as young as early Pridoli. However, graptolites from the underlying formation are Ludlow in age (BOUCOT *et al.*, 1974). More recently, GOUJET (e.g. BOUYX & GOUJET, 1985; in BLAISE *et al.*, 1991) identified *Thelodus parvidens* in the White Rock Formation of the Bear River region of northern Nova Scotia (Annapolis zone of WILLIAMS, in press) dating these formations as of late Ludlow-early Pridoli.

Other Silurian vertebrate microremains have been found in horizons from Nova Scotia. LEGAULT (1968) described acanthodians from the late Silurian Stonehouse Formation of east Arisaig. Some of the scales were referred by DENISON (1979) to *Machaeracanthus*, typically a Devonian genus, and some resemble those of *Nostolepis*. Further material from the Arisaig section is currently being studied and will be the subject of another paper.

This report briefly outlines new material discovered in Lower Silurian strata which is currently under detailed study. A summary of the new material is presented and a detailed description is provided for a new form from the lowest Silurian Clemville Formation on Gaspé Peninsula, Quebec.

GEOLOGY

BOURQUE (1975), BOURQUE & LACHAMBRE (1981) and NOWLAN (1981, 1983) have outlined the geology of that part of the Gaspé Peninsula of Quebec from which one suite of samples came (see Fig. 1). The sites that yielded microvertebrates are on the Clemville River near Port

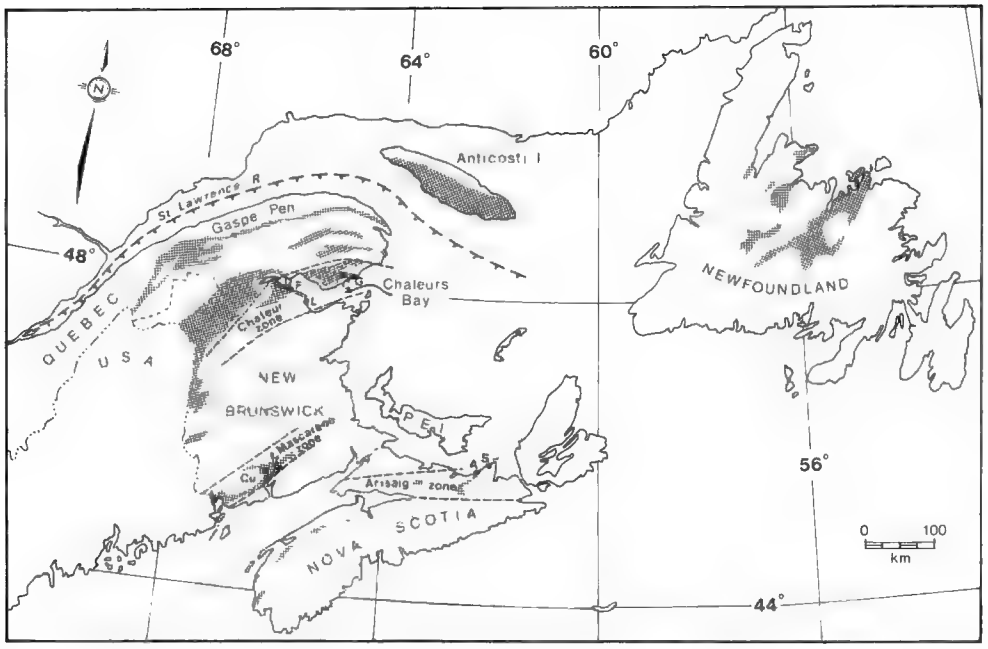


FIG. 1. — Map of eastern Canada showing main outcrops with Lower Silurian strata stippled. Those regional geologic zones of WILLIAMS (in press) that are mentioned in the text are shown bounded by dashed lines. Dots indicate specific sections mentioned in the text and Appendix 1: A, Arisaig coastal section (BOUCOT *et al.*, 1974); C, Petit Port Daniel River section, near Clemville (BOURQUE & LACHAMBRE, 1981); Cu, Cunninghams Brook locality (TURNER, 1986); D, sections at Dickie Point, Dickie Cove and Razor Cove (LEE & NOBLE, 1977); F, Flanagans section (NOBLE, 1976); G, road and railroad cut sections east of Anse aux Gascons (BOURQUE & LACHAMBRE, 1981); L, Limestone Point section (NOBLE, 1976); S, School Brook Cove fault zone (KEPPIE, 1980). Modified from NOWLAN (1983).

Carte du Canada oriental montrant les principaux affleurements. Silurien inférieur en grisé. Les zones géologiques régionales de WILLIAMS (sous presse) qui sont mentionnées dans le texte sont limitées par une ligne en pointillé. Les points indiquent les coupes particulières mentionnées dans le texte et l'Appendice 1. A, coupe côtière d'Arisaig (BOUCOT et al. 1974); C, coupe de Petit Port Daniel River, près de Clemville (BOURQUE & LACHAMBRE, 1981); Cu, localité de Cunninghams Brook (TURNER, 1986); D, coupes de Dickie Point, Dickie Cove et Razor Cove (LEE et NOBLE, 1977); F, coupe de Flanagans (NOBLE, 1976); G, coupes de la route et du chemin de fer à l'Est de l'Anse aux Gascons (BOURQUE & LACHAMBRE, 1981); L, coupe de Limestone Point (NOBLE, 1976); S, zone faillée de School Brook Cove (KEPPIE, 1980). Modifié d'après NOWLAN (1983).

Daniel (NOWLAN, 1983, Fig. 5, sites 2A, B and C). The Clemville Formation is at the base of the Chaleurs Group and contains a good Llandovery A brachiopod zone fauna and conodonts comparable with those of the lowermost Silurian of Anticosti Island. There are also forms assignable to the *Icriodella discreta-deflecta* conodont zone of Britain (Rhuddanian to early Fronian). BOURQUE (1975) interpreted the sediments as shallow water 'platformal' deposits. The Weir Formation vertebrates came from two calcarenite horizons within sandstone units on the north flank of the Clemville anticline. The brachiopod and conodont assemblages in the Weir Formation suggest an early Fronian age. The overlying Anse aux Gascons and Anse à Pierre-Loiselle Formations span the late Llandovery (C4-6) (see NOWLAN, 1983, Fig. 2).

			Québec (Gaspé)		North New Brunswick		South New Brunswick	Nova Scotia
L. SILURIAN	LLANDOVERY		LA VIEILLE FM		LA VIEILLE FM		LONG REACH FM	
		C6	ANSE à PIERRE-LOISELLE	*Thelodus* sp. *Log. scotica* *Log. sibirica* typ. 2 *Log. "cruciformis"*	LIMESTONE POINT FM	*Thelodus parvidens?* *Log. sibirica* typ. 2 *Log. scotica*	*Thelodus parvidens* *Log. sp?*	
		C5	ANSE aux CASCONS FM	helenolepid? *Log. scotica* s.s. *Log. sibirica* type 2 *Log. "cuneata"*				
		C3-4						SCHOOL BROOK COVE: *Log.* cf. *sibirica* *Log. cuneata* group
		C1-2	WEIR FM	*Log. scotica* group *Log. sibirica* *Thelodus?*				
		B1-3	CLEMVILLE FM	*Thelodus?* sp. *Log. scotica* group *Log. sibirica* *Valyalepis crista*	AKMSTRONG BROOK FM	*Log.* cf. *sibirica?*		
		A1-4						
ORD.								

FIG. 2. — Summary of geological formations and microvertebrate assemblages from eastern Canada reported herein.
Synthèse des formations géologiques et des assemblages de microvertébrés du Canada oriental décrits ici.

NOBLE (1976) and LEE & NOBLE (1977) have described the sections in northern New Brunswick from which additional vertebrate material has been derived. NOWLAN (1983) has summarized the conodont biostratigraphy of the Llandovery strata of this region. The microvertebrates were recovered from the uppermost part of the Armstrong Brook Formation and that part of the Limestone Point Formation that correlates best with the Anse à Pierre-Loiselle Formation across Chaleurs Bay to the north.

KEPPIE (1980) discussed the unnamed limestones from the School Brook Cove, Nova Scotia, which are also placed within the early Llandovery (upper Idwian-lower Fronian B1 to C1-2). NOWLAN (in KEPPIE, 1980) identified biostratigraphically diagnostic conodonts and made a preliminary identification of scales of "*Logania*?" and "*Thelodus* species" from two horizons in early Llandovery limestone blocks from the east side of School Brook Cove, Cape George, Nova Scotia (Fig. 1, and see KEPPIE, 1980, Fig. 1 for detailed location). A summary of the geology and age of the new material is given in figure 2 and further details of the sites can be found in the Appendix 1.

NEW MATERIAL AND METHODS

This study provides the first evidence of the earliest Silurian vertebrates in eastern Canada and the first Silurian remains from Quebec. The exposed sections near Port Daniel, Quebec, provide good continuous successions from which to get information on both conodont and thelodont biostratigraphy for the Early Silurian.

The thelodont scales and other microvertebrates reported here were first discovered in the late 1970s to early 1980s following treatment of the Early Silurian limestones for conodonts using the acetic acid technique (e.g. RIXON, 1976). The new assemblages come from the Lower Silurian Chaleurs Group in the Llandovery strata of Gaspé Peninsula; from the Armstrong and Limestone Point Formations, New Brunswick; and from unnamed limestones in the School Brook Cove area, Nova Scotia. All microvertebrate remains were sent to the senior author for further examination. Here we present a preliminary account of the fish remains as outlined by one of us (TURNER, 1991b) at the Studies on Early Vertebrates Symposium held at the Parc de Miguasha, Quebec, in June 1991. This report includes the first formal description of a new genus announced at the symposium and named in honour of a key worker in Early Silurian microvertebrate studies, Dr Valentina N. KARATAJUTE-TALIMAA of Lithuania.

RESULTS: SUMMARY OF NEW MICROVERTEBRATE ASSEMBLAGES

THELODONTI

Loganiida

Loganellia sibirica Karatajute-Talimaa, 1978 from the Clemville and Weir Formations, Quebec; School Brook Cove blocks, Nova Scotia. These scales closely resemble the scales of *Loganellia sibirica* from Tunguska, Siberia (KARATAJUTE-TALIMAA, 1978, tab. XX, Figs. 3-12).

Loganellia sp. cf. *L. sibirica* (*L. sibirica* type 2 in Fig. 2) from the Anse aux Gascons and Anse à Pierre-Loiselle Formations, Quebec, and possibly the Limestone Point Formation, New Brunswick.

Loganellia scotica (TRAQUAIR 1898) from the Clemville and Weir Formations, Anse aux Gascons, Anse à Pierre-Loiselle Formations, Quebec; Limestone Point Formation, northern New Brunswick. TALIMAA & MELIKOV (1987) placed together a group of closely-related scales from the Early Silurian of Russia which presumably share features in common with *L. scotica*; they referred them to "*L.* ex group *scotica*". Certainly scales of *L. scotica* type are typical of the Early Silurian in Scotland; the type locality is the *Jamoytius* horizon of the Patrick Burn Formation, Lesmahagow (RITCHIE, 1963; TURNER, 1984); in the Kilbride Formation of Ireland (TURNER, pers. obs.); in Timan-Pechora and northern Siberia (KARATAJUTE-TALIMAA, 1978); and in England (ALDRIDGE & TURNER, 1975; TURNER, in BLIECK & JANVIER, 1991). We place some of the scales from eastern Canada in the *L. scotica* group and some as *L. scotica sensu stricto* (see Fig. 2).

Loganellia ex gr. *cuneata* from the Clemville region, Quebec and the School Brook Cove beds, Cape George, Nova Scotia. The presumed headscales of *L. cuneata*, called *L. cruciformis*

by GROSS (1967) occur in the Anse à Pierre-Loiselle Formation, Clemville River section, Quebec. This group of thelodont scales which superficially resemble *L. cuneata* (GROSS, 1967) is in need of revision. Scales of this type have been reported from the Early to Late Silurian of Siberia, Tuva and the Baltic region (e.g. KARATAJUTE-TALIMAA, 1978; MÄRSS, 1986a). The scales from eastern Canada are rather slender and resemble those from Siberia. *L. cruciformis* is now sometimes listed as the cruciform scale type if found in association with *L. cuneata* scales (e.g. MÄRSS, 1986a).

Helenolepid?

A few scales of a possible new taxon of *Helenolepis*-like scales come from the left bank section of Petit Port Daniel River, west of Clemville, Quebec, Upper Llandovery Anse aux Gascons Formation, Chaleurs Bay Group. These scales appear closest to *Helenolepis* Karatajute-Talimaa, 1978 known from the Pridoli of Tuva. TALIMAA (1990) has also reported helenolepid scales from the Upper Llandovery of Siberia. A decision on their designation will have to wait until more is known about the Siberian forms and until more material is available for histological analysis.

Katoporida?

Scales of *Valyalepis crista* n. g., n. sp., described below, occur throughout the Clemville Formation, Quebec. Details of localities which yielded the new taxon are given in Appendix I.

Thelodontida?

Thelodus? sp. indet.: Only two scales have been found from the upper 2m of the Clemville Formation and 12.7m above the base of the Weir Formation. One scale in the Anse à Pierre-Loiselle Formation resembles *Thelodus admirabilis* Märss, 1982. These scales are outwardly typical of *Thelodus* (see e.g. GROSS, 1967, taf. 1) but have small notches in the anterior crown rim, a feature which separates them from most known *Thelodus* species. They might also be special cephalo-pectoral or oral scales of a loganiid, which commonly resemble scales of *Thelodus* (e.g. TURNER, 1991a). A decision on their designation will have to wait until more material is available for histological analysis.

Thelodus sp. cf. *T. parvidens*: One scale from the Limestone Point Formation of northern New Brunswick resembles those of the type thelodont. Alternatively, it might be a scale of *Thelodus laevis*.

ANASPIDA?

A few ridged scales in the Limestone Point Formation might belong to a birkeniid anaspid (cf. MÄRSS, 1986a, tab. XXVI). NORFORD (1972) has reported possible Lower Silurian anaspid remains from Greenland; THORSTEINSSON (pers. comm.) has new articulated anaspids from the basal Wenlock of Cornwallis Island, Arctic Canada; and anaspids occur in the late Llandovery of Scotland (RITCHIE, 1963).

GNATHOSTOMES

These remains are still being studied and will not be discussed in detail here but investigated in a future paper. Scales and bone fragments occur in the Clemville and basal Weir Formations

and in the Anse à Pierre-Loiselle Formation; some appear to be acanthodian and some might belong to an acanthodian or a shark; one scale in the latter formation resembles those of *Pilolepis margaritifera* Thorsteinsson, 1973.

A few scales in the Limestone Point Formation might belong to primitive sharks. These scales are rounded with rhomboid bases bearing a basal pulp cavity and neck openings. Other scales and ornamented bone might belong to an acanthodian or placoderm.

SYSTEMATIC PALAEONTOLOGY (S. Turner)

Class THELODONTI
Order KATOPORIDA? Karatajute-Talimaa, 1978
Family KATOPORIDAE? Karatajute-Talimaa, 1970
Genus **VALYALEPIS** n. g.

TYPE SPECIES. — *Valyalepis crista* n. g., n. sp.

DIAGNOSIS. — As for type and only species (see below).

REMARKS. — These scales are characterized by a distinct median raised ridge which may or may not bifurcate towards the anterior margin of the crown and an otherwise relatively smooth crown surface, a combination of which is considered, at this time, to be a feature of generic importance not found in other thelodont scales except to a more advanced level perhaps in phlebolepid scales (see e.g. MÄRSS, 1986a, b).

ETYMOLOGY. — Named in honour of Dr Valentina (Valya) N. KARATAJUTE-TALIMAA for her pioneer work on Palaeozoic microvertebrates, and from *lepis* – scale.

Valyalepis crista n. sp.
(Figs. 3-6)

1991b, new genus: Turner, p. 45.

DIAGNOSIS. — Thelodont with small scales less than 1mm in length. Simple, elongate, diamond or rounded leaf-shaped outline with a small posterior point and one or more pairs of lateral indentations possible; rare lateral lappets. Crown larger than the base. Most body scales have a distinctive crown ornament of a single, raised median rib which usually bifurcates just posterior to the anterior rim: trifurcation is possible. Neck low and smooth. Base oval and annular. Basal growth with deepening can occur. Large, oval, shallowly-concave pulp cavity. Histology of katoporid type (*sensu* GROSS, 1967; TURNER, 1991a): numerous dentine tubules open directly into the pulp cavity. A short canal, which is slightly thicker than the tubules, either single or double, is present in the posterior pulp cavity in some specimens. Crown rim can have minor crenulations. Scales in cross-section resemble a ridged roof. Oral or anterior head scales smaller, low anteriorly with scalloped crown edge rising to a smoother posterior point; posterior neck higher than anterior. Cephalo-pectoral scales more elongate with scalloped crown margin and weaker median rib.

HOLOTYPE — Geological Survey of Canada – GSC103671 from GSC loc. 0-96428 (Fig. 3G-I)

REFERRED MATERIAL. — 5 scales (GSC 103667-103670, 103684, 103686) from the type locality (Figs. 3A-F, 4M, O) and 58 scales (GSC 103672-103683, 103685, 103690-103716 and 108940-108953) from GSC localities 0– 98049, 0-98060-63, 98065-70 (Figs 4, 5, 6). Other material has been used for histological examination. The specimens are reposited in the National Collection of Type Invertebrate and Plant Fossils at the Geological Survey of Canada, Ottawa).

TYPE LOCALITY. — Measured section in Clemville Formation (between 85.5m above the base up to 2m below the top of the formation), Petit Port Daniel River, west of Clemville, Quebec, eastern Canada (C, Fig. 1; see Appendix 1 for details).

TYPE HORIZON. — 2 m below the top of the Clemville Formation, Chaleurs Group (*Distomodus kentuckyensis* zone, lower Llandovery (A3-4 brachiopod zones), Lower Silurian).

ETYMOLOGY. — From *crista* meaning a ridge, in allusion to the shape of the cross section of most scales.

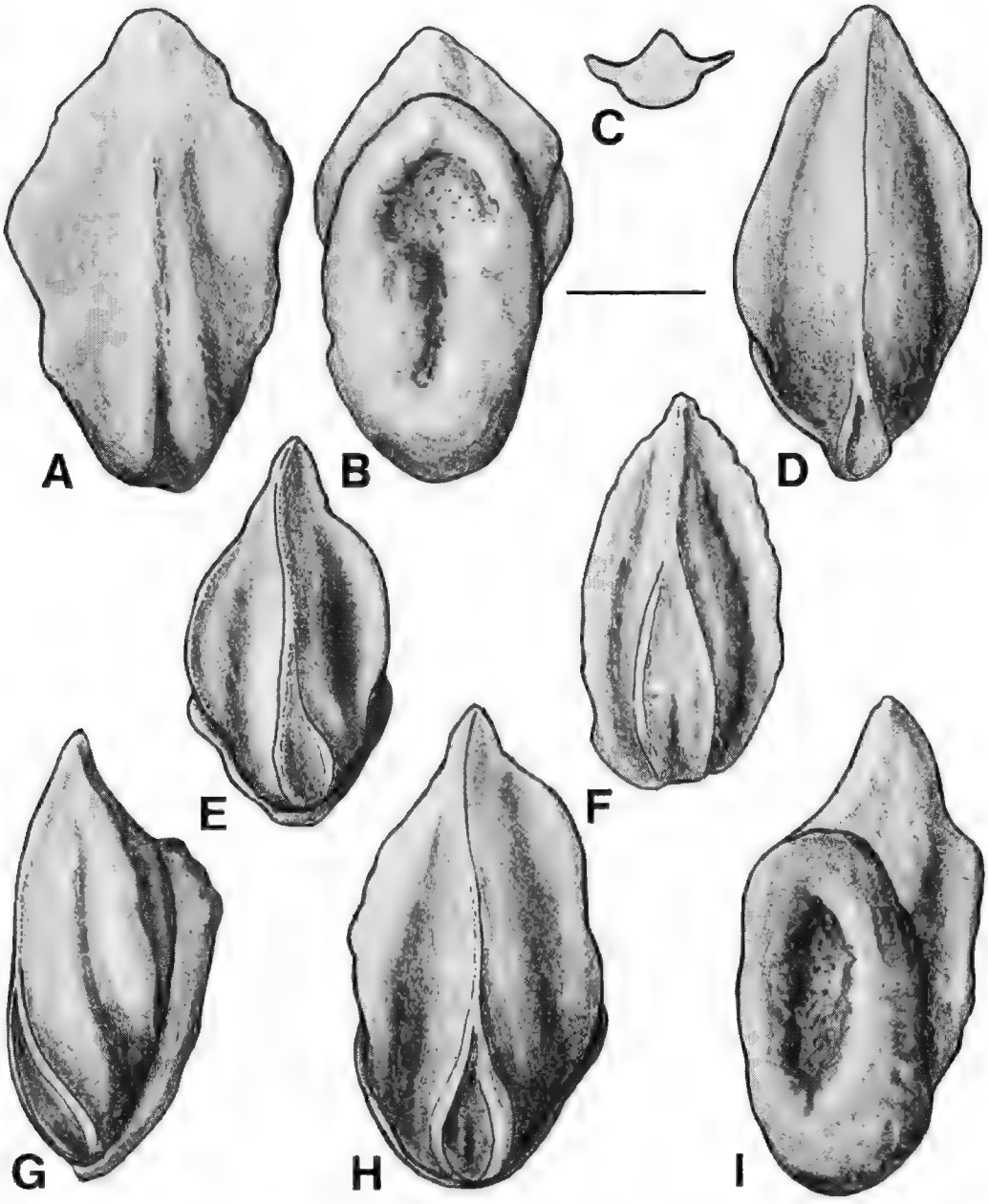


FIG. 3. — *Valyalepis crista* n. g., n. sp.: representative scales from locality GSC loc. 0-96428, upper 2m of Clemville Formation. A-B, GSC 103667; A, dorsal (crown) view; B, ventral (basal) view; C, sketch diagram of cross section of trunk scale (not to scale); D, GSC 103668; E, GSC 103669; F, GSC 103670; D-F, all in dorsal view; G-I, holotype GSC 103671; G, lateral view; H, dorsal view; I, ventral view. Scale bar: 0.2 mm.

Valyalepis crista *n. g., n. sp. : écailles représentatives de la localité GSC loc. 0-96428, 2m du sommet de la Formation de Clemville. A-B, GSC 103667 ; A, vue dorsale (coronale) ; B, vue ventrale (basale) ; C, schéma d'une coupe à travers une écaille du tronc (pas à l'échelle) ; D, GSC 103668 ; E, GSC 103669 ; F, GSC 103670 ; D-F, toutes en vue dorsale ; G-I, holotype GSC 103671 ; G, vue latérale ; H, vue dorsale ; I, vue ventrale. Échelle : 0,2 mm.*

DESCRIPTION

Scales mostly 0.5mm in length (range 0.4– just less than 1mm). Most scales are low, almost flat with the prominent mid rib especially seen in the body scales (Figs. 3D-I, 4, 5). Bases are very shallow in most scales (all are probably from individuals with scales from the same growth generation); deeper rounded bases are rarely seen (Fig. 5.31).

Oral or anterior head scales are small (less than 0.5mm), and generally rounded (Figs. 5.1-7). Some head scales exhibit typical raised posterior point and minor scalloping on anterior crown rim. Rounded head scales can be wider than long (e.g. Fig. 5.6).

Transitional scales also usually have a strong median rib with three to four pairs of coarse lateral ribs (e.g. Figs. 4, 5.9, 22-23). The anterior bifurcation of the midrib can extend half way back along the crown and a pair of fly-away posteriorly-pointing lateral wings can be present (e.g. Figs. 4, 5.15). One large transitional (cephalo-pectoral) scale has two pairs of deeply indented scallops and a prominent bifurcated anterior rim (Fig. 5.17).

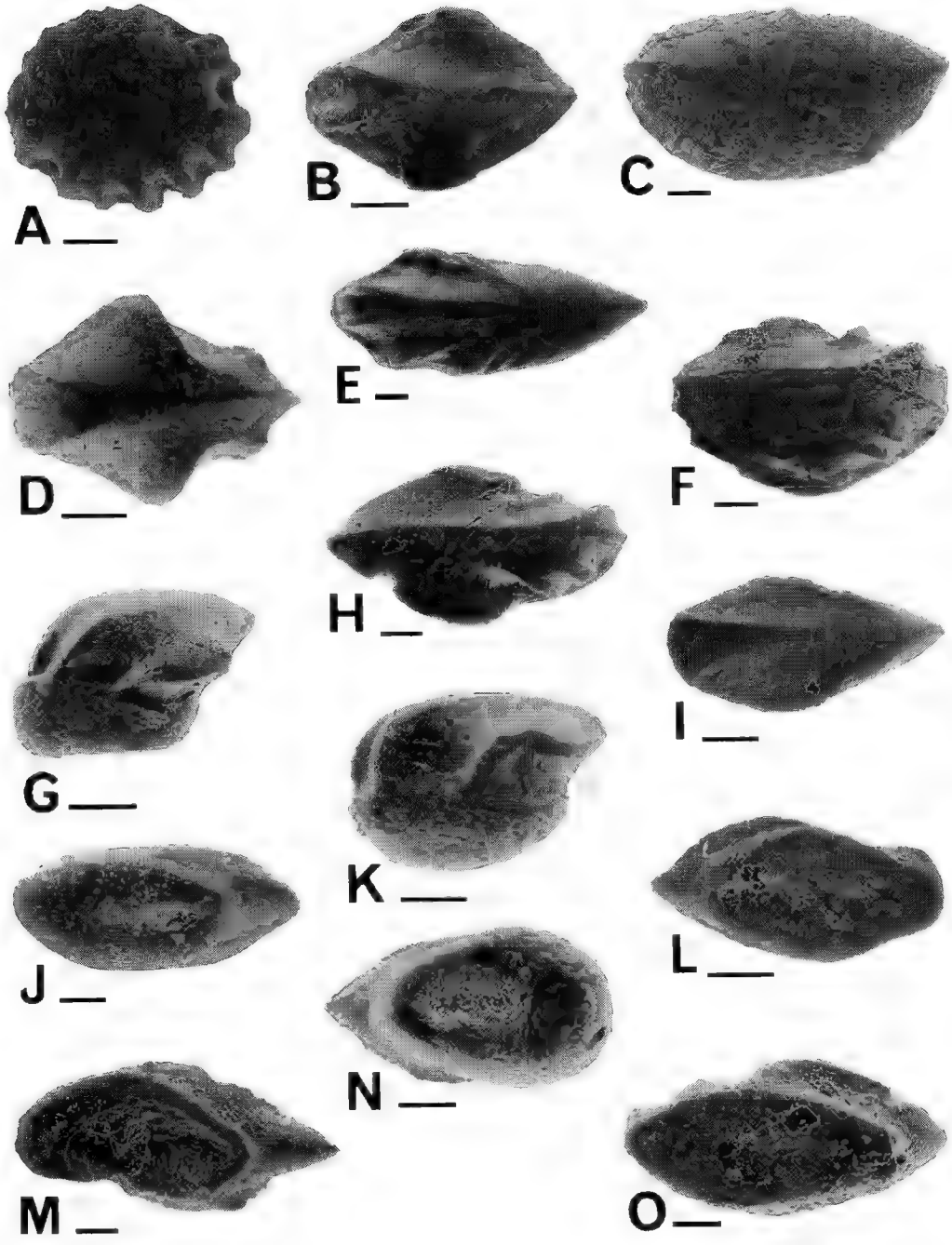
In many scales the central pair of crown ribs converges in the midline at a point less than one third, up to one half of the way along the crown, producing a triangular mid-section (e.g. Figs. 4, 5.21). One or two pairs of anterior notches can be seen. The scales are characterized by a pagoda-like cross-section which results from the high median rib on the crown (Fig. 3C). Figure 5 shows the range of variation and details of variety in crown ornament and shape in the Clemville scales. Possible placement into oral, cephalo-pectoral and postpectoral (*sensu* MÄRSS, 1982; 1986a, b) is indicated. Differentiation into the pinnal, and precaudal scale groups of MÄRSS (op. cit.) could not be decided.

HISTOLOGY

The scales are generally thin and not altered. The histological structure was discerned using anise oil application (KARATAJUTE-TALIMAA, 1978) and by making a few thin sections of a few broken scales. The small size and thinness of the scales, however, makes the former technique more successful; no diagnostic thin sections are yet available. Most scales are young in the growth series, having shallow bases, sometimes with only a thin annular ring, and a large open pulp cavity (Fig. 6B). The pulp cavity can be oval, elliptical or mushroom-shaped (Figs. 3B, I, 5.25, 6A-C). As noted above, very few scales exhibit the older stage with deeper basal growth. In ventral view, the numerous dentine tubules or canals can be seen opening directly into the pulp cavity (Figs. 3B, I; 5.25, 6A-C). They are scattered evenly over the inner surface although the shape of the pulp cavity can be mushroom-shaped with the "stalk" anteriorly and thus the tubule or canal openings can form a restricted pattern within the cavity (e.g. Figs. 3B, 6A, C). In the postero-ventral point of the pulp cavity a slightly larger opening can be seen which seems to be the opening of a wider dentine canal or a short, narrow pulp canal (e.g. Fig. 6A). This short canal, directed back into the distal point of the crown, can be seen in a few of the transparent scales.

DISCUSSION

The style of histology seems closest to the "*Katoporus*" type of GROSS (1967). *Valyalepis* thus may be the oldest katoporid recognised to date. However, from the fineness of the tubules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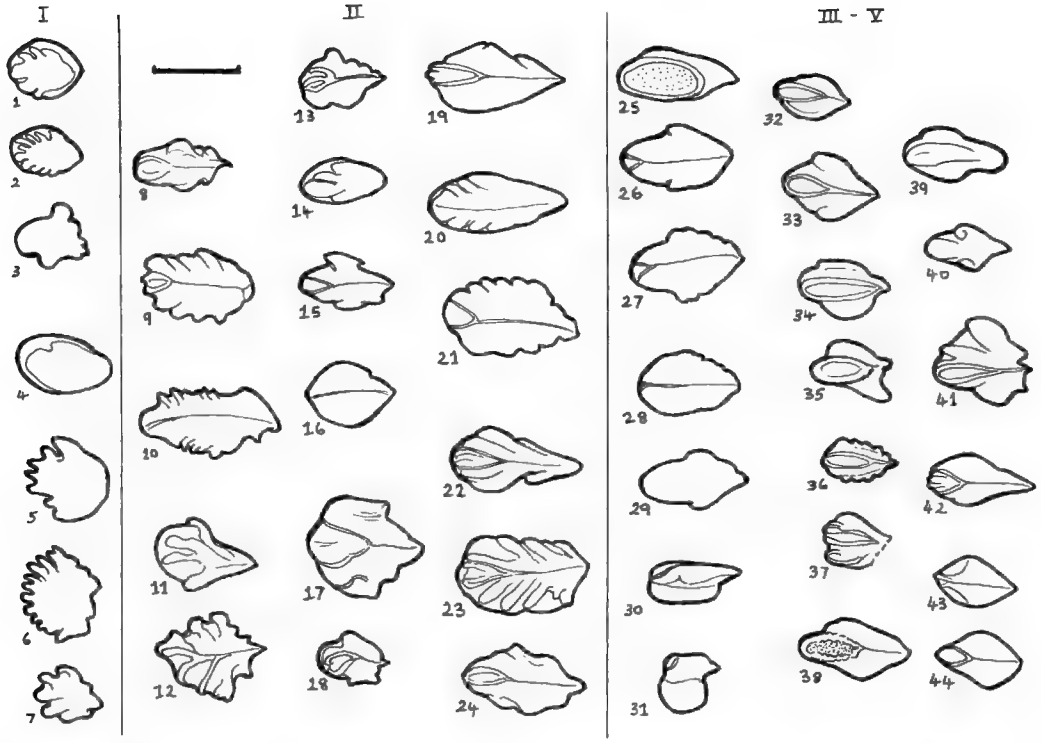

FIG. 5. — *Valyalepis crista* n. g., n. sp.: sketches showing range of variation in morphology of scales based on specimens from GSC localities from the Clemville Formation. Scale bar: 0.5mm. Specimens 1-5: GSC 103690-103694; 6: GSC103672; 7-29: GSC 103695-103716; 30: GSC 103678; 31-44: GSC 108940-108953. Sample localites: GSC loc. 0-98049 – 20, 26-29; GSC loc. 0-98060 – 1-3, 8, 14, 17, 21-22, 30, 32-33, 34-35, 42; GSC loc. 0-98061 – 4, 15-16, 43; GSC loc. 0-98062 – 5, 19, 23, 31, 37, 44; GSC loc. 0-98063 – 39; GSC loc. 0-98065 – 7, 11-12, 40-41; GSC loc. 0-98066 –6; GSC loc. 0-98068 – 9-10, 13, 18, 25; GSC loc. 0-98070 – 24, 38.

Valyalepis crista *n. g., n. sp. : dessins montrant le domaine de variation morphologique des écailles, fondés sur des spécimens des localités GSC de la Formation de Clemville. Échelle : 0,5 mm. Spécimens 1-5 : GSC 103690-103694 ; 6 : GSC103672 ; 7-29 GSC 103695-103716 ; 30 : GSC 103678 ; 31-44 : GSC 108940-108953. Localités d'échantillonnage : GSC loc. 0-98049620, 26-29 ; GSC loc. 0-98060-1-3, 8, 14, 17, 21-22, 30, 32-33, 34-35, 42 ; GSC loc. 0-98061 - 4, 15-16, 43 ; GSC loc. 0-98062 - 5, 19, 23, 31, 37, 44 , GSC loc. 0-98063 - 39 ; GSC loc 0-98065 - 7, 11-12, 40-41 ; GSC loc. 0-98066 - 6 ; GSC loc. 0-98068 - 9-10, 13, 18, 25 ; GSC loc. 0-98070 - 24, 38.*

FIG. 4. — SEM photographs of scales of *Valyalepis crista* n. g., n. sp. A, possible oral scale, GSC 103672; B. post-pectoral trunk scale, GSC 103673; C, cephalopectoral scale, GSC 103674; D, cephalopectoral scale, GSC 103675; E, possible caudal scale, GSC 103676, F, post-pectoral trunk scale, GSC 103677; G, cephalopectoral scale in lateral view, GSC 103678; H, GSC 103679; I, post-pectoral trunk scale, GSC 103680; J, basal view to show narrow pulp cavity, GSC 103681, K, lateral view, GSC 103682; L, basal view, GSC 103683; M, basal view showing wide pulp cavity, GSC 103684; N, basal view, GSC 103685; O, basal view, GSC 103686. Scale bar for all: 100 µm, except E: 200 µm.

Photographies au microscope électronique à balayage d'écailles de Valyalepis crista *n. g., n. sp. A, écaille orale possible, GSC 103672 , B, écaille post-pectorale du tronc, GSC 103673 , C, écaille céphalopectorale, GSC 103674 ; D, écaille céphalopectorale, GSC 103675; E, écaille caudale possible, GSC 103676; F, écaille post-pectorale du tronc, GSC 103677; G, écaille céphalopectorale en vue latérale, GSC 103678 ; H, GSC 103679 ; I, écaille post-pectorale du tronc, GSC 103680 ; J, vue basale montrant la cavité pulpaire étroite, GSC 103681 ; K, vue latérale, GSC 103682 ; L, vue basale, GSC 103683; M, vue basale montrant la large cavité pulpaire, GSC 103684 ; N, vue basale, GSC 103685 ; O, vue basale, GSC 103686. Échelle : 100 µm, sauf E : 200 µm.*

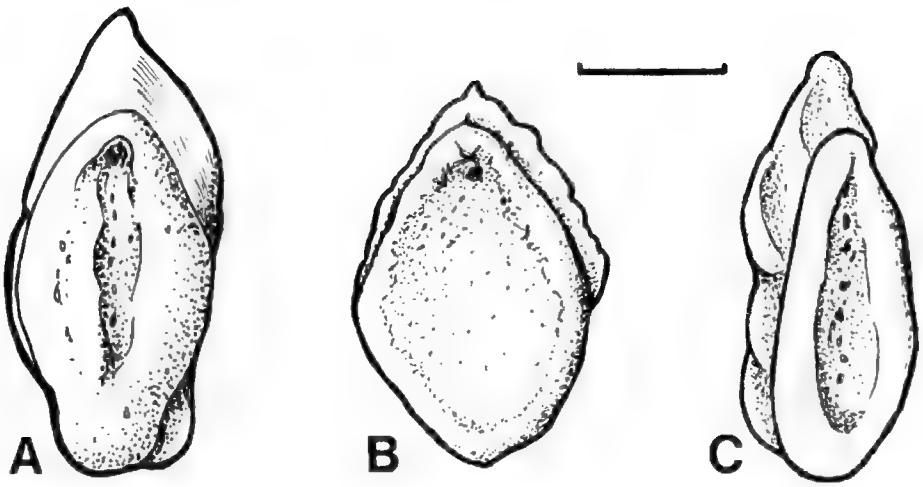

FIG. 6. — Sketches of the base of three scales of *Valyalepis crista* n. g., n. sp. to show the structure of the pulp cavity and dentinal tubule/canal openings. A-B, GSC 103687-103688 from GSC loc. 0-98070; C, GSC 103689 from GSC loc. 0-98066. Scale bar: 0.2 mm.

Dessins de la base de trois écailles de Valyalepis crista *n. g., n. sp. montrant la structure de la cavité pulpaire et des ouvertures des canaux/tubules de dentine. A-B, GSC 103687-103688 de la loc. GSC 0-98070 ; C, GSC 103689 de la loc. GSC 0-98066. Échelle : 0.2 mm.*

it is possible that these could be interpreted as dentine tubules and not canals and thus *Valyalepis* might be regarded as a relatively advanced or specialised loganiid (*sensu* TURNER, 1991a). Head and transitional scales, if identified correctly as such, do not differ greatly from some loganiid scales. However, in the general style of the trunk scales with a median ridge on a thin crown and almost no base the scales of the new genus resemble those of *Phlebolepis*, considered by most to be an advanced katoporid (e.g. KARATAJUTE-TALIMAA, 1978). Thus it is possible that *Valyalepis* is a close, plesiomorphic relative of *Phlebolepis*.

SUMMARY AND CONCLUSIONS

Previous to this account, Early Llandovery thelodonts had been found in North Timan, Siberia and Tuva (ex Tuvainska A.R.) (e.g. MOSKALENKO, 1968; KARATAJUTE-TALIMAA, 1978; VALIUKEVICIUS *et al.*, 1983; VLADIMIRSKA *et al.*, 1986; TALIMAA & MELIKOV, 1987). There had been speculation that thelodonts originated in the Siberian or Tuvan regions (Angaraland) (BLIECK & GOUJET, 1978; TURNER & TARLING, 1982). The fauna reported here adds a new dimension to the picture of the evolution of the earliest thelodonts with the presence of several loganiid species and a new, possible primitive katoporid, *Valyalepis crista*, as well as other fish in eastern Canada in the former Chaleur zone, contemporary, if not older than remains from elsewhere. Upper Ordovician thelodonts have been reported from Timan-Pechora (e.g. in MÄRSS, 1989) and may occur in Canada (BARNES, SPJELDNAES, in BLIECK & JANVIER, 1991), but neither

find has yet been documented. TALIMAA (1991, pers. comm.) has indicated the close similarity of one of the Late Ordovician forms from Russia to *Valyalepis*. TALIMAA (1990) reported the presence of *L.* ex gr. *scotica* in the Late Ordovician of Russia. Now, there is a strong suggestion of closer links between the Chaleur zone and Timan-Pechora/western Siberia to allow for the dispersal of these primarily shallow-water marine forms.

The presence of a possible thelodontidid in the Clemville Formation of Quebec (Chaleur zone), if confirmed, is the earliest record for the group. *Thelodus* species appear definitely in the late Llandovery of Europe and in the Long Reach Formation (possible late Llandovery-Wenlock) of southern New Brunswick within the Mascarene zone. They occur commonly in the Arisaig and Annapolis zones by Ludlow-Pridoli times. A possible scale of *Thelodus parvidens* in the Limestone Point Formation hints at the contemporaneity of part of this formation with the Long Reach Formation of southern New Brunswick and the Early Silurian appearance of this species. The similarity of *Loganellia sibirica* group scales in the Anse à Pierre-Loiselle and Limestone Point Formations confirms that the latter is of late Llandovery (C5-6) age.

The eastern Canadian thelodonts found in the Chaleur, Mascarene and Arisaig zones in the Early Silurian closely resemble those from Timan-Pechora and parts of Siberia (e.g. KARATAJUTE-TALIMAA, 1978; TALIMAA, 1990). By late Llandovery, however, a similar thelodont fauna is more widespread, being found in the Chaleur zone, southern Britain, and in the Irish-Scottish-Norwegian belt (Midland Valley terrane) (TURNER pers. obs.). The earliest Silurian Clemville Formation fauna appears to contain endemic elements and to be distinct from the others recorded here. If *Valyalepis* proves to be a primitive katoporid then that group of thelodonts is present in the eastern Canadian region (Chaleur zone) as well as probably in Timan-Pechora.

The exposed sections on the Gaspé Peninsula, Québec, provide good potential for a detailed conodont and microvertebrate biostratigraphy of the Lower Silurian. The thelodonts found there represent some of the oldest known to date and the other microvertebrates comprise anaspid?, shark?, placoderm? and acanthodian? remains, some of which are the oldest records for gnathostome fishes.

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APPENDIX

Detailed localities are provided only for the illustrated material of the new taxon erected in this paper; all are in the Clemville Formation, Chaleurs Bay Group. The localities identified by letters on figure 1 are described below by province and formation. For summary correlation chart see NOWLAN (1983, Fig. 2).

QUEBEC

CLEMVILLE FORMATION

Locality C on figure 1: the samples from the Clemville Formation all come from sections along the Petit Port Daniel River, just west of the village of Clemville near Port Daniel, on the

Gaspé Peninsula. A sketch map of the locality has been published by BOURQUE & LACHAMBRE (1981, Fig. 16). The formation is 110m thick and is exposed on either side of an anticline cored by the unconformably underlying Mictaw Group. Rhuddanian to Aeronian *Stricklandia typica* phylozone (Llandovery A3-4) and *I. discreta-I. deflecta* conodont zone. For details of conodont ranges see NOWLAN (1981, Fig. 5).

GSC loc. 0-96428, 2m below top of formation, north flank of Clemville anticline, latitude 48°10'42"N, longitude 65°01'34"W : 22 specimens (TURNER, 1984) – *V. cristata*; *Loganellia sibirica*, *L.* sp?, *Thelodus* sp?, indeterminate bone?

GSC loc. 0-98049, 3m below top of formation, below power transmission line, latitude 48°10'36"N, longitude 65°01'29"W: 14 specimens – *V. crista*; *Loganellia sibirica*, *L.* ex gr. *scotica*, acanthodian? scale, shark scale?

GSC loc. 0-98060 72m above base of formation, south flank of Clemville anticline, latitude 48°10'33"N, longitude 65°01'13"W: 30 specimens – *V. crista*; *Loganellia sibirica*, *L.* sp. cf. *L. scotica*, indeterminate thelodont? scale.

GSC loc. 0-98061, 72.5m above base of formation, south flank of Clemville anticline, latitude and longitude as for 0-98060. 10 specimens – *V. crista*; *Loganellia sibirica*, *L.* ex gr. *scotica*.

GSC loc. 0-98062 73.8m above base of formation, south flank of Clemville anticline, latitude and longitude as for 0-98060 : 32 specimens – *V. crista*; *Loganellia sibirica*, *L.* sp. cf. *L. scotica*, *L.* ex gr. *scotica*, thelodont or acanthodian? scale, phyllocarid.

GSC loc. 0-98063 75m above base of formation, south flank of Clemville anticline, latitude and longitude as for 0-98060: 12 specimens – *V. crista*; *Loganellia sibirica*, phyllocarid.

GSC loc. 0-98064 – 77m above base of formation, south flank of Clemville anticline, latitude and longitude as for 0-98060: 1 specimen – thelodont? (missing).

GSC loc. 0-98065 –79m above base of formation, south flank of Clemville anticline, latitude and longitude as for 0-98060: 39 specimens – *V. crista*; *Loganellia sibirica*, *L.* sp. cf. *L. scotica*, *L.* ex gr. *scotica*, 1 small indeterminate scale?

GSC loc. 0-98066 – 80m above base of formation, south flank of Clemville anticline, latitude and longitude as for 0-98060: 12 specimens – *V. crista*; *Loganellia sibirica*, *L.* sp. cf. *L. scotica*, *L.* ex gr. *scotica*, 1 piece bone?

GSC loc. 0-98067 81m above base of formation, south flank of Clemville anticline, latitude and longitude as for 0-98060: 22 specimens - *V. crista*; *Loganellia sibirica*, *L.* sp. cf. *L. scotica*, *L.* ex gr. *scotica*, 1 acanthodian? scale.

GSC loc. 0-98068 82m above base of formation, south flank of Clemville anticline, latitude and longitude as for 0-98060: 30 specimens – *V. crista*; *Loganellia sibirica*, *L.* sp. cf. *L. scotica*, *L.* ex gr. *scotica*, indeterminate bone?

GSC loc. 0-98069 83.8m above base of formation, south flank of Clemville anticline, latitude and longitude as for 0-98060: 13 specimens – *V. crista*; *Loganellia sibirica*.

GSC loc. 0-98070 85.5m above base of formation, south flank of Clemville anticline, latitude and longitude as for 0-98060: 19 specimens – *V. crista*; *Loganellia sibirica*, 1 bone?

WEIR FORMATION

Locality C as described above under Clemville Formation.

ANSE AUX GASCONS FORMATION

Locality C as described above under Clemville Formation.

ANSE À PIERRE-LOISELLE FORMATION

Locality C as described above under Clemville Formation.

Locality G: Roadcut on Highway 132 near Gascons, southern Gaspé Peninsula, latitude 48°12'20"N, longitude 64°49'30"W; railway cut 500m southeast of highway section, latitude 48°12'13"N, longitude 64°49'05"W (see BOURQUE & LACHAMBRE, 1981, Figs. 2, 12).

NEW BRUNSWICK

ARMSTRONG BROOK FORMATION

Locality L: Coastal exposure at Limestone Point, northern New Brunswick, latitude 47°48'54"N, longitude 65°43'34"W (see NOBLE, 1976, Figs. 1, 2).

LIMESTONE POINT FORMATION

Locality D: Dickie Cove Brook and Dickie Point, west of Jaquet River, northern New Brunswick, latitude 47°57'07"N, longitude 66°07'45"W (see LEE & NOBLE, 1976, Figs. 1, 2).

Locality F: Coastal exposure at Flanagans, west of Quinn Point, northern New Brunswick, latitude 47°55'06"N, longitude 65°57'18"W (see NOBLE, 1976, Figs. 1, 2).

Locality L as described above under Armstrong Brook Formation.

LONG REACH FORMATION

Locality Cu: Cunninghams Brook locality, southern New Brunswick, approximate latitude 45°24'N, longitude 66°19'W (see STETSON, 1928; TURNER, 1986).

NOVA SCOTIA

ARISAIG GROUP

Locality A: Arisaig coastal section west of Arisaig; long section starting at latitude 45°45'20"N, longitude 62°10'36"W and ending at latitude 45°44'09"N, longitude 62°12'40"W (see BOUCOT *et al.*, 1974 for details).

FORMATION UNCERTAIN

Locality S: School Brook Cove fault zone, latitude 45°53'00"N, longitude 61°55'06"W (see KEPPIE, 1980 for detailed locality).

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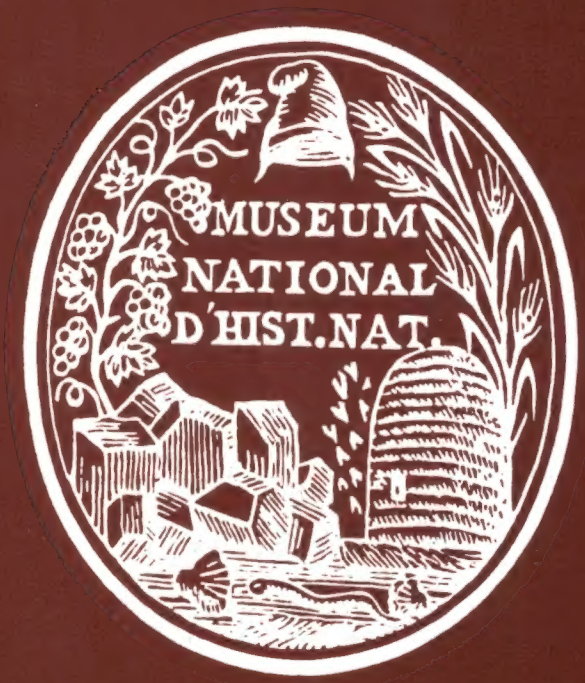
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